WHAT DETERMINES SEX ROLES IN MATE SEARCHING?

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In a seminal paper, Hammerstein and Parker (1987) described how sex roles in mate searching can be frequency dependent: the need for one sex to perform mate searching is diminished when the opposite sex takes on the greater searching effort. Intriguingly, this predicts that females are just as likely to search as males, despite a higher potential reproductive rate by the latter sex. This prediction, however, is not supported by data: male mate searching prevails in nature. Counterexamples also exist in the empirical literature. Depending on the taxon studied, female mate searching can arise in either low- or high-density conditions, and suggested explanations differ accordingly. We examine these puzzling observations by building two models (with and without sperm competition). When sperm competition is explicitly included, male mate searching becomes the dominant pattern; when it is excluded, male mate searching predominates only if we assume that costs of searching are higher for females. Consequently, two hypotheses emerge from our models. The multiple-mating hypothesis explains male searching on the basis of the ubiquity of sperm competition, and predicts that female searching can arise in low-density situations in which sperm can become limiting. It can also explain cases of female pheromone production, where males pay the majority of search costs. The sex-specific cost hypothesis predicts the opposite pattern of female searching in high-density conditions, and it potentially applies to some species in which sperm limitation is unlikely.

KEY WORDS: Mate search, multiple mating, pheromone, sex roles, sperm competition.

In most sexually reproducing organisms, finding a conspecific mate requires some form of physical activity: at least the gametes, but often the organisms themselves, have to be mobile. Effort invested into mate searching, however, can be costly (Gwynne 1987; Acharya 1995; Grafe 1997; Okuda 1999; Melville et al. 2003; Kasumovic et al. 2007). Searching effort can be defined as a costly activity that evolves to improve mate-encounter rates, whether this involves physical movement or some other form of active behavior (e.g., calls or pheromone production). For individuals of one sex, the problem is solved—in the sense that mate finding does not require any effort—if the opposite sex performs sufficient searching. Because males of a typical species benefit from multiple mating more than females (Bateman 1948), they are typically expected to be the mate-searching sex, and females should consequently spend zero effort in mate searching.

There are two reasons, however, why mate searching deserves closer attention: one theoretical and one empirical. First, we lack a general theoretical explanation for the fact that males often take on the searching role. In a seminal paper, Hammerstein and Parker (1987) considered the mate search conundrum using a game theoretical approach. Their "mobility game" attempted to explain why one sex should invest greater search and movement effort than the

other, and why males tend to be the ones that end up assuming the greater effort (i.e., females typically "win" the game). Prima facie, one might expect males to be the more mobile sex if females invest more in offspring and represent a limiting resource for males (Parker 1978). Hammerstein and Parker (1987) found, however, that a searching male strategy and a searching female strategy were alternative evolutionary stable strategies (ESSs). The relative investment in offspring did not matter to the model outcome, and females could "lose" both the game over parental investment and the one over effort spent in searching.

In other words, theory explains why one sex should expend greater search effort than the other (instead of both sexes investing equally), but it does not explain *which* of the sexes this should be. Thus, although it may sound intuitive that differences in gametic investment and consequent asymmetries in parental care explain why males search, modeling does not confirm this but predicts, instead, divergent searching patterns (here we use "divergence" as a shorthand for a pattern in which current sex differences are magnified consequences of slight ancestral deviations in searching patterns). Since Hammerstein and Parker (1987), very little theoretical effort has been spent on this problem. The only examples we are aware of consider highly taxon-specific questions, such as payoffs that depend on the time of day in lekking insects (Ide and Kondoh 2000). This lack of progress is surprising, given that our theoretical understanding of sex roles has otherwise advanced considerably (e.g., Clutton-Brock and Parker 1992; Parker and Simmons 1996; Queller 1997; Kokko and Monaghan 2001).

The second reason for further analysis is an empirical one. There are relatively few studies explicitly devoted to studying the relative roles of males and females as mate searchers, and, among the handful that have considered the topic, there is a lack of consensus regarding factors that favor mate searching by females. On the one hand, evidence suggests that females should expend greater search effort if search costs are low. Such a situation often appears to correspond to high density. In fiddler crabs *Uca beebei*, for example, females increase their mate-search activities when crab densities are high; the abundance of nearby burrows at such densities reduce female search costs by allowing them to escape quickly from potential predators (deRivera et al. 2003). Arguments linking reduced search costs with female mate searching have also been suggested for moths (Greenfield 1981). Here, the adaptive reasoning is based on the contention that females are the limiting sex and thus should not be expected to pay high costs of searching.

On the other hand, evidence from other taxa suggests that high density can favor male, rather than female, searching (Kokko and Rankin 2006). In several species of frogs and orthoptera, for example, males, at low densities, use acoustic signals to attract searching females but, at higher densities, may switch over to a roaming strategy (Alexander 1975; Wells 1977; Davies and Halliday 1979; Byrne and Roberts 2004). Although one should keep

in mind taxon-specific explanations, such as the need to avoid male–male competition caused by silent satellite frogs that join calling males (Lucas and Howard 1995), this alternative response to density has also led to a suggested general explanation of sex roles (Wickman and Rutowski 1999): males should be the default searching sex because they have the most to gain from multiple matings but, at low density, females are selected to begin searching because any delay in becoming fertilized is costly for a female (see also Kokko and Mappes 2005).

More generally, high search effort by females is not always linked to situations when costs are low. Evidence suggests that females are capable of expending considerable effort on mate searching even when confronted with high search costs. This is seen, for example, in the cardinal fish *Apogon niger*, in which increased mobility by mate-searching females late in the breeding season is correlated positively with their rate of disappearance attributed, apparently, to mortality by predatory flounder and lizardfish (Okuda 1999). During their short lifetime, female butterflies *Coenonympha pamphilus* incur significant time costs by traveling to visit males at the lek (Wickman and Jansson 1997). In that species, it has been suggested that the fitness costs suffered by females, in the form of reduced fecundity, are ameliorated by potential indirect benefits of mating with males at the lek (Wickman and Jansson 1997). A similar argument has been made for pronghorn *Antilocapra americana*, an ungulate in which females in estrus spend considerable amounts of energy moving between harems before mating (Byers et al. 2005). Finally, there are also cases where both sexes invest in mate-finding traits. In many arthropods, for example, females produce pheromones, and males follow these chemical trails (Greenfield 1981; Cardé and Baker 1984; Cardé and Hagaman 1984; Takács et al. 2002; Melville et al. 2003; Nahrung and Allen 2004).

Here, our goal is to extend earlier theory and provide models that can produce the observed diversity of searching outcomes, including the "female pheromone" case with large investment in males and a small, but important, investment in females. We do not base our model on particular features of any taxa. Instead, we aim at maximum generality by keeping the life history as simple as possible, and by varying parameters such as the mate-encounter rate from extremely small values (representing slow moving, widely dispersed, solitary organisms) to very high ones (representing, e.g., colonial species). We begin by defining mate searching effort in a way that excludes nonadaptive correlations between mobility and mate finding, and then proceed to building self-consistent (Houston and McNamara 2005) models of searching effort, one without, and another with, sperm competition. Our models validate the symmetry argument by Hammerstein and Parker (1987) that searching by either sex can diminish selection for mate searching in the other. However, our models also lead to two different hypotheses that can be used to explain the greater prevalence of

male (vs. female) searching, and we will examine their explanatory power in the Discussion.

Self-Consistency and the Definition of Mate Searching

We develop two self-consistent models in which males and females attempt to locate each other for the purpose of mating. Self-consistency means that fitness must be evaluated by taking into account the fact that total reproduction by males should equal total reproduction by females, because every individual has one mother and one father. This simple fact, termed the Fisher condition by Houston and McNamara (2005), has been shown to be surprisingly important for developing correct predictions in conceptual models of reproductive behaviors (e.g., Queller 1997; Webb et al. 1999; Houston and McNamara 2002, 2005; Kokko and Jennions 2003; Arnqvist 2004; Houston et al. 2005).

In both models, we assume that females and males are free to invest any amount of effort (i.e., zero or positive) into mate searching. We denote this investment by x for females and y for males. Investment in mate searching is assumed to increase the rate with which the searching individual finds members of the opposite sex, and to impose costs on the searcher. These costs are expressed as a reduction in some other component of fitness. In our particular model formulation, we assume that this component is survival (i.e., mate searching carries a mortality cost), but there is no reason why the conclusions could not be extended to other fitness costs as well (e.g., fecundity).

Our cost-based definition of investment in mate searching resembles the definition of parental investment, namely, care that is performed at a cost to future offspring production (Trivers 1972). To avoid drawing erroneous conclusions from our model, it is important to focus on these costs, because they help to distinguish between behaviors that are selected for other reasons but happen also to improve mate-encounter rates, and behaviors that are selected *because* they improve mate-encounter rates. For example, consider a butterfly in which females have to locate resources required for the larvae to develop (e.g., a suitable host plant for oviposition). Females are obviously selected to fly until they find such a resource. For a male, it may be optimal to wait at a resource patch if he has found one, or to intercept a female that is making her way to the resource. The observation preceding a mate encounter is that a female flies toward a male; however, this should not, sensu stricto, be classified as investment in mate searching by the female, because no extra cost is incurred on top of what she would have expended in any case in her quest to find a suitable egg-laying patch (see also Groddeck et al. 2004). Thus $x = 0$ in such a case. If, on the other hand, she traveled to a male lek before flying to the resource patch, the extra travel time involved presumably carries some direct cost on survival and/or fecundity.

Consequently, one should classify the female's behavior as investment in mate searching, $x > 0$.

Self-Consistent Model with No Sperm Competition

We base our models on the concept of reproductive value and invasion fitness: a strategy of mate searching can invade if, and only if, it yields higher fitness than the resident strategy (Metz et al. 1992). Fitness in this setting is a weighted sum of the number of different types of individuals that the focal individual contributes to the population, weighted by the reproductive value of each individual type (e.g., McNamara and Houston 1986, 1996; Taylor 1990). Our model is based on a continuous-time setting, for the reason that males and females may spend quite dissimilar times in parenting activities. This implies that an individual may contribute, at any given time, to the future population in three ways: by actual offspring production, by surviving itself without changing state, or by surviving and changing state. All these options are taken into account in the concept of reproductive value, following the method outlined in Härdling et al. (2003).

Following a tradition in the literature of sex role evolution (Clutton-Brock and Parker 1992; Parker and Simmons 1996; Wiklund et al. 1998; Kokko and Monaghan 2001; Kokko and Ots 2006), we define the relevant states as "time in" and "time out" for both sexes (Fig. 1). In our first model, mating occurs every time a male and a female meet in time in. There is only one mating preceding the production of offspring, and we assume that females cannot store sperm. We thus exclude sperm competition and multiple mating within one reproductive cycle of a female. Following mating, g offspring of each sex are produced. Both parents then enter a time out stage (sensu Clutton-Brock and Parker 1992), which makes them unable to mate again before a certain time has elapsed.
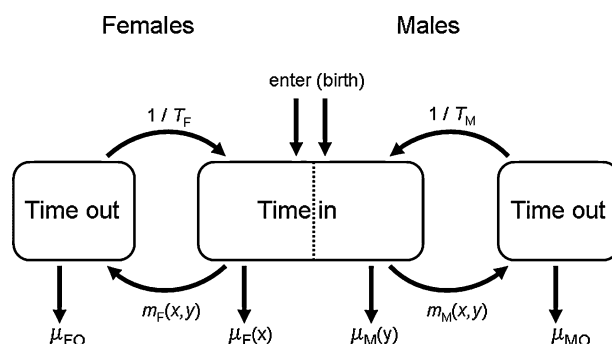

Figure 1. Flow diagram of the model. Females and males encounter each other when they are in time in; after mating, both sexes enter a time out stage, but the length of this can be different for the two sexes. Mating rates can differ between the sexes, too, because of a different number of males and females in the time in stage.

Time out activities may involve parental care, replenishing sperm stores, or any other task that must be performed before reproduction is possible again. Because sexes often differ greatly in their parental investment, the duration of the time out period can be very different for the sexes, which also limits their potential reproductive rate (PRR) (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992). For example, with mortality rate 0.1 and time out $T_F = 1$ for females, females can reproduce, on average, approximately 10 times before dying. By contrast, males with time out $T_M = 0.01$ can experience reproductive events at a 100-fold rate compared with that of females during the same time frame (were they able to find the necessary number of females with whom to mate; see Queller 1997; Kokko and Jennions 2003; Arnqvist 2004).

Female search effort, x, and male search effort, y, both influence the mating rate of females and males who are in time in. Females mate at a rate $m_F(x,y)$, and males at a rate $m_M(x,y)$. These rates are increasing functions of both x and y. In a population with an unbiased operational sex ratio (OSR), these two rates are equal. However, males and females can enjoy different mating rates if the OSR is biased toward one or the other sex. In a population consisting of β males: females in the time in state, the mating rate for the two sexes can be written as $m_F(x,y) = Mf(x,y)\sqrt{\beta}$ and $m_M(x,y) = Mf(x,y)/\sqrt{\beta}$, where $f(x,y)$ describes the searching outcome, that is, how mate-encounter rates respond to mate-searching behavior of the two sexes. Because searching improves mate-encounter rates, we have $\partial f/\partial x > 0$, and $\partial f/\partial y > 0$, but many different functional forms are possible. For example, $f(x,y) = xy$ assumes that both sexes must perform some searching before they can find each other at all, whereas $f(x,y) = x+y$ describes a species in which mates encounter each other frequently as soon as one of the sexes searches sufficiently. The parameter M ($M > 0$) is used to compare mate-encounter rates between populations or species (*cf*. Kokko and Monaghan 2001; Härdling and Kaitala 2005; Kokko and Mappes 2005). Importantly, the operational sex ratio β depends on searching effort, $\beta = \beta(x,y)$, because searching influences mating rates and consequently also sex-specific mortalities and the amount of time individuals spend in the time in state. Equation (3) in Kokko and Monaghan (2001) gives the value of β once mating rates are known.

To keep in line with our definition of mate searching as an investment that carries costs, we introduce a mortality cost during time in (other types of cost could be equally easily added to the model, such as mortality during time out, lengthening the duration of time out, or reducing fecundity for females). Thus, for females, the mortality during time in is $\mu_F(x)$, which is an increasing function of x, whereas during time out the mortality is fixed, μ_{FO}. For males, the corresponding values are $\mu_M(y)$ and μ_{MO}. Note that in a continuous-time formulation, the mortalities can take any value

$\mu > 0$: values exceeding unity simply mean an expected life span below 1.

The evolution of female and male behavior can be tracked by building a matrix for reproductive values that develop in continuous time (for details of the method see Härdling et al. 2003):

$$d\mathbf{v}/dt = \mathbf{v}\mathbf{Q}. \qquad (1)$$

Here, $\mathbf{v} = (v_{FO}, v_{FI}, v_{MO}, v_{MI})$ marks the vector of reproductive values of females in time out, females in time in, males in time out, and males in time in. The transition matrix $\mathbf{Q}$ is given by

$$\mathbf{Q} = (q_{ij}) =$$
$$\begin{pmatrix} -\dfrac{1}{T_F} - \mu_{FO} & m_F & 0 & 0 \\ \dfrac{1}{T_F} & m_F(g-1) - \mu_F & 0 & m_M g \\ 0 & 0 & -\dfrac{1}{T_M} - \mu_{MO} & m_M \\ 0 & m_F g & \dfrac{1}{T_M} & m_M(g-1) - \mu_M \end{pmatrix},$$
$$(2)$$

where, for brevity, we use notation m_F for $m_F(x,y)$, μ_F for $\mu_F(x)$, etc. The elements of this matrix give the continuous-time per capita rates of changing from one state to another, in which the states are listed in the same order as in the vector $\mathbf{v}$ but now columns indicate the current state and rows the future state. For example, column 1 lists two possible transitions made by a female in the time out state. She may return to time in, which happens at rate $1/T_F$, and because this means changing the reproductive value from v_{FO} to v_{FI} (i.e., add v_{FI}, remove v_{FO}), the rate $1/T_F$ appears as an addition in the second column (the second element gives v_{FI} in $\mathbf{v}$) but as a subtraction in the first row (corresponding to v_{FO} in $\mathbf{v}$). The female may also die, which happens at a rate μ_{FO}, and leads to a loss of reproductive value v_{FO} and no gain—that is, the rate μ_{FO} appears as an additional loss in row 1. Other columns are similarly derived. Reproduction happens at rate m_F and m_M for females and males, respectively, and this adds reproductive values of offspring $g\,v_{FI}$ and $g\,v_{MI}$ to the matrix equations. Note that offspring values do not depend on who the parents were, thus we ignore the possibility that mate searching evolves as a means to sample several potential mates and mate with the ones of highest quality; see Discussion for this limitation.

Härdling et al. (2003) produced a method to calculate the selection differentials in a continuous-time setting with several states. When a resident population (using x^*, y^*) is at population equilibrium, the reproductive values $\mathbf{v}^*$ satisfy $d\mathbf{v}^*/dt = 0$ (Härdling et al. 2003). The equilibrium requirement yields the following relationships between reproductive values of states:

$$v_{FI}^*/v_{FO}^* = 1 + \mu_{FO}T_F, \qquad (3a)$$

$$v_{MI}^*/v_{MO}^* = 1 + \mu_{MO}T_M, \tag{3b}$$

$$\text{and} \quad v_{MI}^*/v_{FI}^* = \frac{\mu_F}{m_F} - \frac{g-1}{g} - \frac{1}{g(1+\mu_{FO})}. \tag{3c}$$

Consider a mutant female with strategy x in a population in which x^* and y^* are in use. Assume that the mutant is rare, which means that its search effort x changes its mating rate $m_F(x)$ via its effect on $f(x,y^*)$, but the operational sex ratio β experienced by the mutant is not significantly altered by its presence but determined by population-wide behavior x^* and y^*, thus $\beta = \beta(x^*,y^*)$. (Obviously the population may shift to a new x^* and y^* as the eventual consequence of successful mutant invasion, and β will thus be recalculated for each pair $\{x^*, y^*\}$ when determining evolutionary trajectories). The strength of selection at $\{x^*, y^*\}$ is a partial derivative of the mutant's reproductive value $\partial v_{FI}(x,x^*)/\partial x$ $|_{x=x^*, y=y^*}$, where

$$v_{FI}(x, x^*) = e^{-r^*}[v_{FO}^* q_{11} + v_{FI}^* q_{21} + v_{MI}^* q_{41}]$$

$$= e^{-r^*}[v_{FO}^* m_F(x) + v_{FI}^*[m_F(x)(g-1) - \mu_F(x)] + v_{MI}^* m_F(x)g]. \tag{4}$$

Here, r^* is the continuous-time growth rate of the resident population, which equals $r^* = 0$ for a population at equilibrium. Note that equation (4) is a continuous-time version of mutant reproductive values such as, for example, eq. 17 in Pen et al. (1999). Using equations (3a-c) and (4), we find that the selection differential for female searching equals, up to a constant of proportionality,

$$S_F = g\frac{1}{m_F}\frac{\partial m_F}{\partial x} - \frac{1}{\mu_F}\frac{d\mu_F}{dx}. \tag{5a}$$

A similar derivation gives the male selection differential

$$S_M = g\frac{1}{m_M}\frac{\partial m_M}{\partial y} - \frac{1}{\mu_M}\frac{d\mu_M}{dy}. \tag{5b}$$

The conditions $S_F > 0$ and $S_M > 0$ select for increased mate searching in females and males, respectively. We will derive evolutionary trajectories assuming that searching in the two sexes evolves independently (no genetic covariances between male and female searching).

NO SPERM COMPETITION: RESULTS

The interpretation of equations (5a,b) gives a surprising conclusion: a difference in the time out of the two sexes is not reflected in the equations at all. Nor does the species-specific mate-encounter rate M influence solutions: whereas it influences m_F and m_M, it cancels out in the LHS of equations (5a,b).

How should the independence of searching roles from reproductive effort (time out) be understood? The term $1/m_F \, \partial m_F/\partial x$ gives the proportional increase in female mate–encounter rates for a certain proportional increase in investment in mate searching. The corresponding term for males is $1/m_M \, \partial m_M/\partial y$. Because the
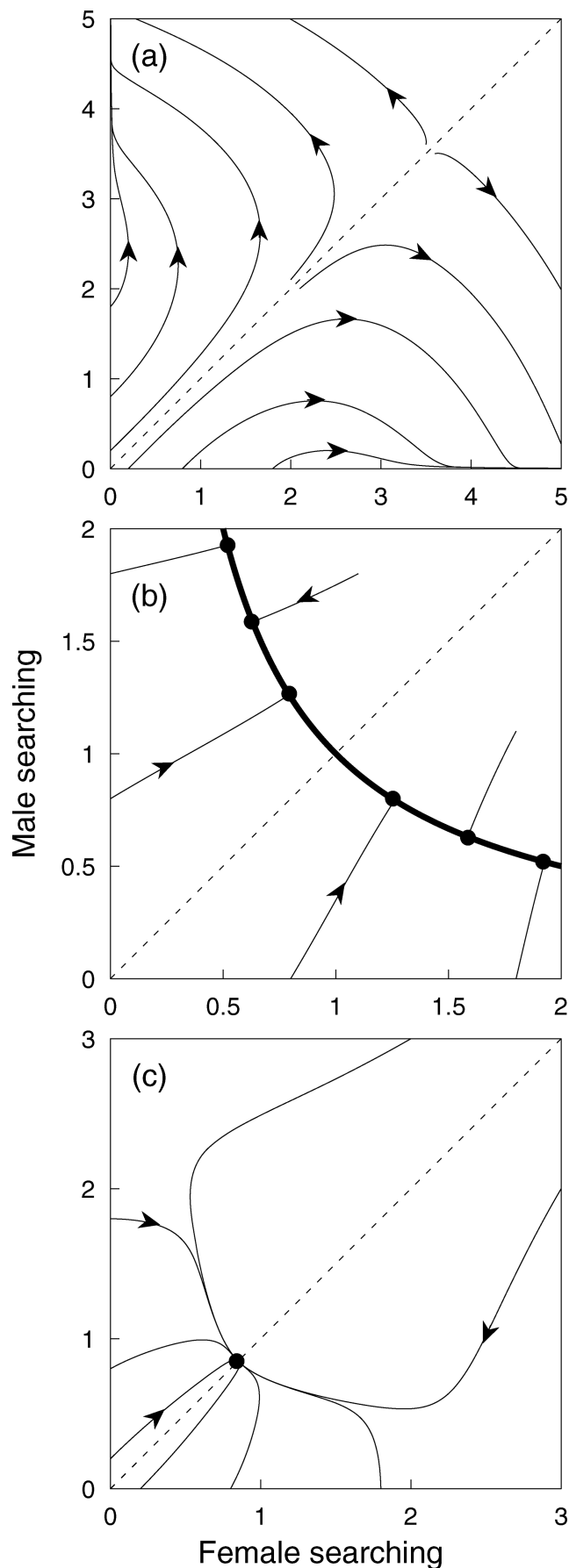
total reproduction in each of the two sexes is the same, and every mating leads to the same expected number (g) of offspring production, there must be equally many reproductive events for females as there are for males; they are also equally valuable. Thus, a given increase (say 1%) in the mating rate gives the same proportional increase in an individual's fitness, regardless of which sex the individual belongs to, or whether mate finding is easy or difficult.

Nevertheless, equations (5a,b) allow for the possibility that one sex performs the majority, or all, of the mate searching. As a whole, individuals of a given sex are selected to search more if their mortality is high ($1/\mu$ is low), if the increase in mortality by doing more searching is relatively low ($d\mu/dt$), if mate finding is currently a slow process ($1/m$ is high), and if a significant increase in mate-encounter rates can be achieved by increasing investment in searching (high $\partial m_F/\partial x$ or $\partial m_M/\partial y$). The last two facts mean that one sex can rely on effort by the other sex. If, for example, the outcome of searching is given by $f(x,y) = x+y$, then $1/m_M$ $\partial m_M/\partial y$ will be proportional to $1/(x+y)$. The more females search, the smaller is the incentive for males to do so ($1/(x+y)$ decreases with increasing x), and vice versa.

However, this does not automatically lead to the two equilibrium states of either male or female searching. Hammerstein and Parker (1987) pointed out that frequency dependence can imply divergent searching roles. Another mechanism inherent in equations (5a,b) acts against divergence; however, searching costs may favor searching in the sex that currently spends little effort. The sex that already invests a lot in mate searching will have high mortality as a result of doing so, and if searching has strongly accelerating costs, it is then more likely that further increases in searching are selected against in this sex. Accelerating costs mean that a little searching can be performed without great mortality risk, and only much more intensive searching carries significant costs. Such cases lead to solutions where both sexes invest equally much in mate searching (Fig. 2).

The importance of the shape of the cost function is shown by a comparison between cases where the mortality increase with mate searching is fairly linear (Fig. 2a), accelerating (quadratic; Fig. 2b), or strongly accelerating (Fig. 2c). In the first case, we predict that only one sex searches, and initial, incidental factors determine which one it is (Fig. 2a). In the second case, there is a line of neutrally stable equilibria, and populations approach any point along this line, again depending on starting conditions of ancient populations. Here, both sexes may search, but they will do so to a different degree: female mate searching is inversely proportional to male mate searching. In the third case, both sexes converge toward a single equilibrium, where they invest equal effort into mate searching (Fig. 2c).

Intuitively, one would imagine that widely differing parental roles (very different T_F and T_M) should give an a priori reason for males to search more than females. In our fully self-consistent

life-history model, we have used a modeling approach that has become one of the standard ways to predict sex role asymmetries (Clutton-Brock and Parker 1992; Parker and Simmons 1996; Kokko and Monaghan 2001). Yet we simply reproduced one central feature of the influential model by Hammerstein and Parker (1987): the images in Figure 2 are symmetrical with respect to the diagonal; thus, there is a fundamental symmetry between the sexes and either sex can end up as the searcher.

It is possible, however, to make the equilibrium of one sex (say, males) be approached more easily than the other. This is achieved by altering the sex-specific parameter values. For example, increasing the female cost of searching by 50% compared with males, shifts the basins of attraction from a symmetrical case (Fig. 3a) to one where evolution more easily proceeds toward male searching (Fig. 3b). Arguing that searching is more costly for males produces an equally strong shift in the direction of female searching (not shown).

Introducing Sperm Competition

A close inspection of the time in–time out modeling framework, above, reveals a potentially unrealistic feature: females always commence reproduction as soon as they have mated once. Although this may be true for some taxa (speckled wood butterflies *Pararge aegeria* typically mate once and then spend the rest of their lives looking for places to lay their eggs: Gotthard et al. 1999), in many species females often mate multiply before any offspring are produced (Jennions and Petrie 2000). This introduces sperm competition, and means that some (often many) matings do not lead to fertilization.

We now introduce a biologically determined minimum time spent in mating activities—the mating window. For our argument it does not matter if it is asynchronous or synchronous between females; in the model it is kept asynchronous. The mating window is included in time in, and females spend it acquiring multiple matings. Offspring can be sired by any male who mates with the

Figure 2. Evolutionary trajectories without sperm competition, when evolutionary change per generation is proportional to the LHS of equations (5a) for females and (5b) for males. The dashed diagonal indicates equal searching by males and females. In (a), selection always favors increased searching effort in the sex that initially searches more. In (b), there is a continuum of neutral equilibria indicated with the heavy solid line, and examples of single equilibria are indicated with dots. Parameters: $T_F = 1$, $T_M = 0.01$, $M = 1$ (although these parameters do not influence solutions as long as there is no sperm competition, see equations (5a, b), $g = 2$, $f(x,y) = x + y$, $\mu_{FO} = \mu_{MO} = 0.1$, and (a) $\mu_F(x) = 0.1 (1 + x^{1.2})$ and $\mu_M(y) = 0.1 (1 + y^{1.2})$, (b) $\mu_F(x) = 0.1 (1 + x^2)$ and $\mu_M(y) = 0.1 (1 + y^2)$, (c) $\mu_F(x) = 0.1 (1 + x^{2.5})$ and $\mu_M(y) = 0.1 (1 + y^{2.5})$.
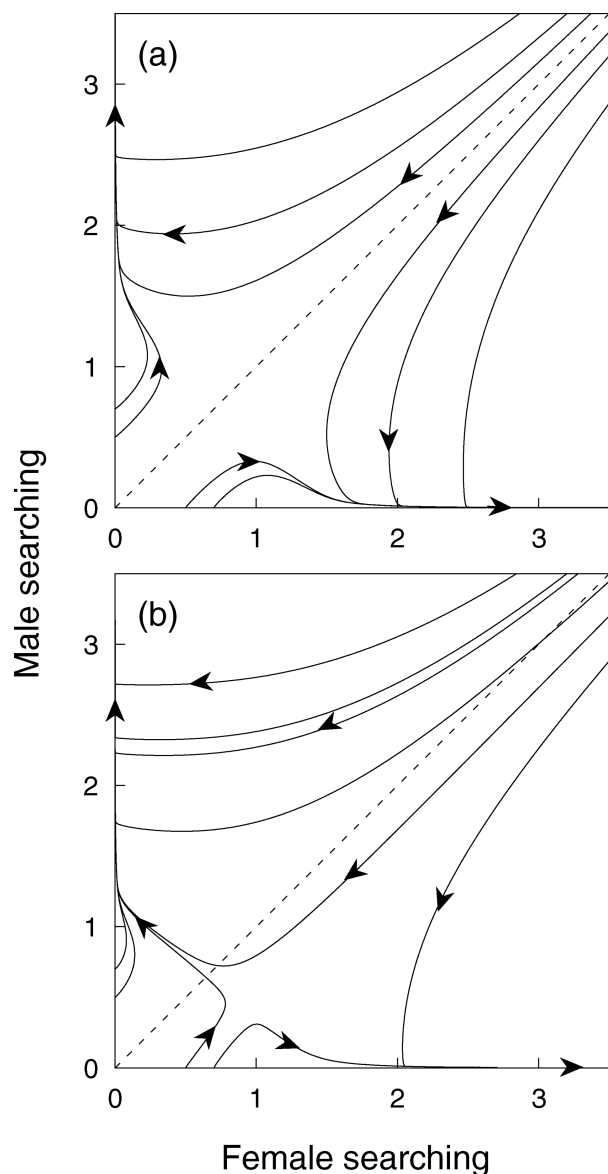
Figure 3. Evolutionary trajectories without sperm competition can become asymmetrical if costs of searching differ between the sexes. Solutions and parameter values are calculated as in Figure 2b, but now with a nonlinear searching outcome $f(x,y) = \sqrt{x+y}$, and (a) equal costs for each sex, $\mu_F(x) = 0.1\,(1 + x^{1.2})$ and $\mu_M(y) = 0.1\,(1 + y^{1.2})$, or (b) female search cost is 50% higher, $\mu_F(x) = 0.1\,(1 + 1.5x^{1.2})$ and $\mu_M(y) = 0.1\,(1 + y^{1.2})$.

female during the mating window. The duration of the mating window can be arbitrarily defined (we use unity). The duration can be short: for example, in frogs, the mating window for a female could be simply the time it takes to release all of her eggs. During this time, several males may be trying to amplex the female, resulting in multiple matings (Byrne and Roberts 2000). In a seasonally breeding organism that can store sperm, on the other hand, the mating window can be a whole year, if a female lays eggs in the spring and uses sperm from males she has encountered up to

a year before. Nevertheless, she may not have encountered many males, if the mate-encounter rate M during this year has been small (e.g., a result of infrequent, perhaps once-a-year nuptial flights).

To make biological sense, this means that the mean number of matings during a mating window, which we denote by N, and the species-specific mate-encounter rate, M, should covary across species. Such a correlation will emerge in our examples, but the number of matings will also increase if either females or males search efficiently (high x and/or y). Inclusion of the mating window means that the OSR calculation (β from eq. 3 in Kokko and Monaghan 2001) becomes an approximation. To ensure that the approximation remains sufficiently accurate, we use low mortality values compared with the length of the mating window.

Because mate encounters are an intrinsically random process, there is a chance that the female spends the mating window without meeting anyone (Kuussaari et al. 1998; Rhainds et al. 1999; Kokko and Mappes 2005), and in that case we assume that she cannot reproduce before she has completed another mating window. Denoting by P the probability that at least one mate has been found during a mating window, and taking note that each window is unity in length, her rate of commencing reproduction from the time in state now equals P. If males are found as a Poisson process with a mean value of $m_F(x,y)$ (which implies $N = m_F(x,y)$), a female will be unsuccessful in locating a male with probability $e^{-m_F(x,y)}$. Therefore, $P = 1 - e^{-m_F(x,y)}$.

The selection differential for females (eq. 5a), up to a proportionality constant, now takes the form

$$
\begin{aligned}
S_F &= g\frac{1}{p}\frac{\partial p}{\partial x} - \frac{1}{\mu_F}\frac{\partial \mu_F}{\partial x} \\
&= b_F\frac{\partial m_F}{\partial x} - \frac{1}{\mu_F}\frac{\partial \mu_F}{\partial x}, \quad \text{where} \quad b_F = g\frac{e^{-N}}{1 - e^{-N}}.
\end{aligned}
\tag{6}
$$

For males, the situation is different. They will suffer from reduced mating success in each mating when females mate multiply, which correctly takes self-consistency into account, but the gains still remain linear: every additional mating improves reproductive success equally much. From each mating with a female, males gain g offspring if the female mates with no other males during the mating window, $g/2$ offspring if she mates once with someone else, $g/3$ if twice, and so on. The expected gain from each mating is obtained from the Poisson distribution,

$$
\sum_{i=0}^{\infty} \frac{g}{i+1} e^{-N}\left(\frac{N^i}{i!}\right) = g\frac{1 - e^{-N}}{N},
\tag{7a}
$$

which gives the male selection differential

$$
S_M = b_M\frac{\partial m_M}{\partial y} - \frac{1}{\mu_M}\frac{\partial \mu_M}{\partial y}, \quad \text{where} \quad b_M = g\frac{1 - e^{-N}}{m_M N}.
\tag{7b}
$$

The terms b_F and b_M relate mating success to offspring production, that is, they are the slopes of the Bateman gradient (Bateman
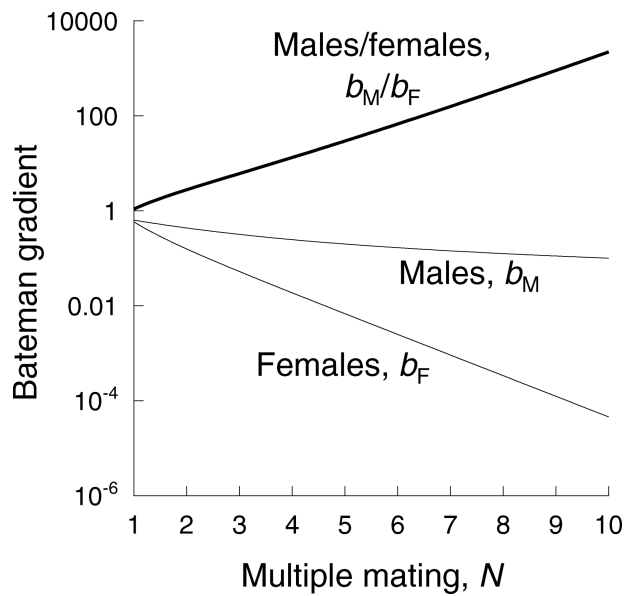
Figure 4. The Bateman gradients, that is, the reproductive bene-fits b_M and b_F for female and males, respectively, from improved mate-encounter rates, and the ratio b_M/b_F, for different values of the average number of matings per mating window, N. The de-crease in both b_F and b_M with N reflects that each mating becomes less important as a determinant of fitness. However, the decrease in b_F is much steeper, therefore, $b_M/b_F > 1$, which implies stronger selection for males to search for mates. Figure is calculated with $g = 1$ and $m_M = 1$. A lower value of m_M (e.g., due to a male-biased OSR) would further exaggerate the difference between b_M and b_F, while g has no effect on b_M/b_F.

1948). The ratio b_M/b_F, describing how much more males ben-efit from finding additional mates than females, increases very strongly with multiple mating (Fig. 4). When one mating window offers an abundance of mating opportunities, most matings are superfluous to females: they do not make a difference to whether she can commence reproduction or not, leading to a shallow slope $\partial p/\partial x$ and therefore a small b_F. For males, each mating also brings about smaller expected fitness gains when there is much sperm competition (b_M decreases with N), but every mating, neverthe-less, contributes to additional paternity chances; b_M therefore stays above b_F, the difference increasing with N (Fig. 4).

SPERM COMPETITION: RESULTS

Once sperm competition is included in the model, mate-encounter rates have a strong influence on investment in mate searching (Fig. 5), and the solutions show sexual asymmetries (Fig. 5). High mate-encounter rates (M) lead to solutions close to the lower left corner in Figure 5a, and they indicate little or no searching by females and significant investment in mate searching by males. The value of N, the average number of males a female mates with, is high in these cases. Low mate-encounter rates, on the other hand, lead to very high investment in searching by both sexes, and
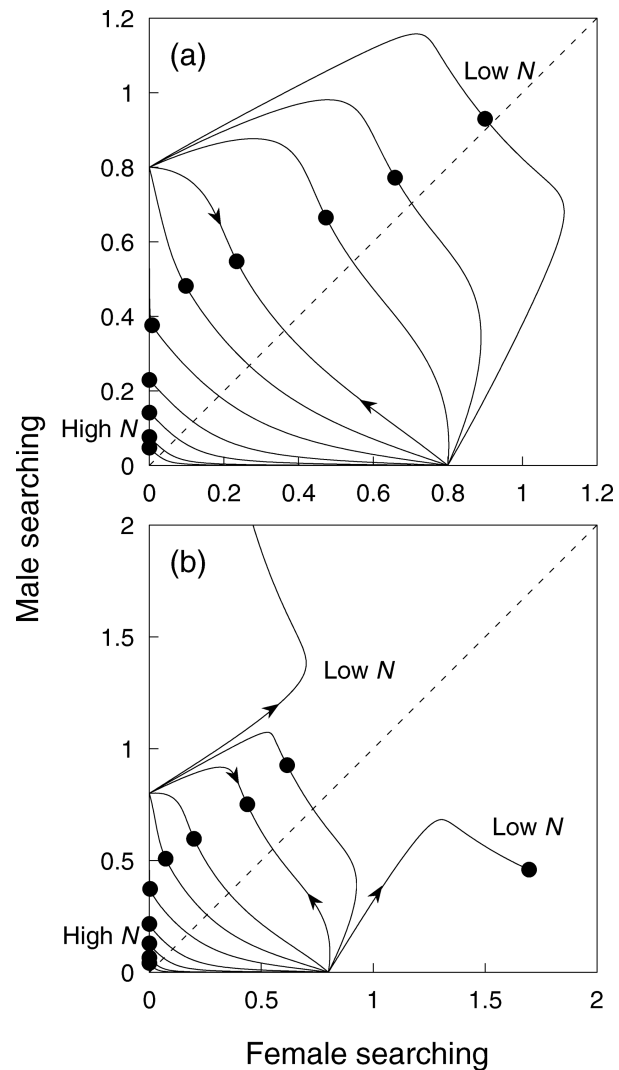

Figure 5. Evolutionary trajectories with sperm competition. Solu-tions and parameter values as in Figure 2b, but now the different curves do not correspond to different starting points $\{x,y\}$ but to different values of species-specific mate-encounter rate, M. M takes values, from left to right, $M = 100, 50, 20, 10, 5, 3, 2, 1, 0.5,$ and 0.1. In (a), costs accelerate as in Figure 2b: $\mu_F(x) = 0.1\ (1 + x^2)$ and $\mu_M(y) = 0.1\ (1 + y^2)$. In (b), costs are more linear than in (a): $\mu_F(x) = 0.1\ (1 + x^{1.8})$ and $\mu_M(y) = 0.1\ (1 + y^{1.8})$. Except for extremely low mate-encounter rates in (b), there is a single equi-librium in each case, and males search more than females. At the equilibrium marked with a dot, the value of N becomes (from left to right) (a) 432, 170, 50, 19.9, 7.9, 4.4, 2.9, 1.5, 0.78, and 0.19, and (b) 359, 148, 46, 18.5, 7.6, 4.2, 2.8, 1.4, 0.77, and (for the female-searching equilibrium) 0.37. Note that females search almost as much as males when low M limits multiple mating (equilibria with low N).

increasing symmetry in effort spent by both males and females (dots near the right end of Fig. 5a). More intensive mate searching does not fully compensate for the rarity of mate encounters, as N stays low at this end of Figure 5a.

It is notable that the same outcomes are approached, regardless of whether females or males were assumed to be the originally searching sex (Fig. 5a). In other words, including sperm competition reduces the tendency for sex roles to be divergent (Figs. 4, 5a). However, if costs have a similar shape that produced divergent roles in the model without sperm competition—that is, little acceleration and thus little "extra" cost for the already searching sex to search more—and if the mate-encounter rate M is low, then divergence can be found even when sperm competition is included (Fig. 5b). Females are not very likely to find several males during one mating window when M is low, which explains the resemblance to the scenario without sperm competition. For example, the lowest value of M considered in Figure 5b ($M = 0.1$) will retain female searching at equilibrium if they were initially the searching sex. At this equilibrium, $N = 0.37$, such that females will not find a male in $\exp(-0.37) = 69\%$ of all their attempts to complete a mating window, and only 5% of females mate multiply.

The model can also be applied to cases where mate location is extremely difficult unless both sexes indicate their presence in some way to members of the opposite sex. This is seen, for example, in many insect systems where mate finding is mediated by pheromones produced by females to attract mate-searching males. In some extreme cases, sex differences in mobility (e.g., ability to fly) mean that females are entirely dependent on searching males who detect and locate the "calling" females (Alcock 1981). There may often be remarkable asymmetry in the effort expended by each sex. Females often only need to release minute quantities of pheromone to elicit a strong response from patrolling males. The cost of pheromone production has been little studied but is generally presumed to be small (Greenfield 1981; Cardé and Baker 1984; Svensson 1996; but see Blows 2002). Males, on the other hand, usually develop extreme mechanisms to follow these trails (e.g., extreme sensitivity to pheromone compounds, Angioy et al. 2003), and may often suffer considerable mortality risks following the pheromone signal (Acharya 1995; Svensson 1996).

Figure 6a shows evolutionary trajectories when the searching outcome is multiplicative, $f(x,y) = xy$, which necessitates some effort by both sexes before $f(x,y) > 0$ is reached. Unsurprisingly, both sexes now spend some effort in mate location, but the overall shape of the solutions stays similar to that of Figure 5: solutions become fairly symmetrical only once M is so small that multiple mating becomes fairly rare. When multiple mating is common, males perform the majority of mate-locating tasks. Figure 6b shows the effect of searching on individual mortalities. The effort that females accept to spend will have minute costs: they evolve to accept a mortality increase of less than 0.01%, when they find, on average, 10 or more mates (two leftmost dots in Fig. 6b). Males, in the meanwhile, accept much higher costs. However, if an average female finds less than four males during a mating window, mortality increases of more than 10% become acceptable for both

sexes, and in extreme cases ($N = 1.28$ in the rightmost dot, Fig. 6b, indicates an $\exp(-1.28) = 27.8\%$ risk of remaining unmated) both females and males can perform activities that double their mortality, if these improve mate-encounter rates sufficiently.
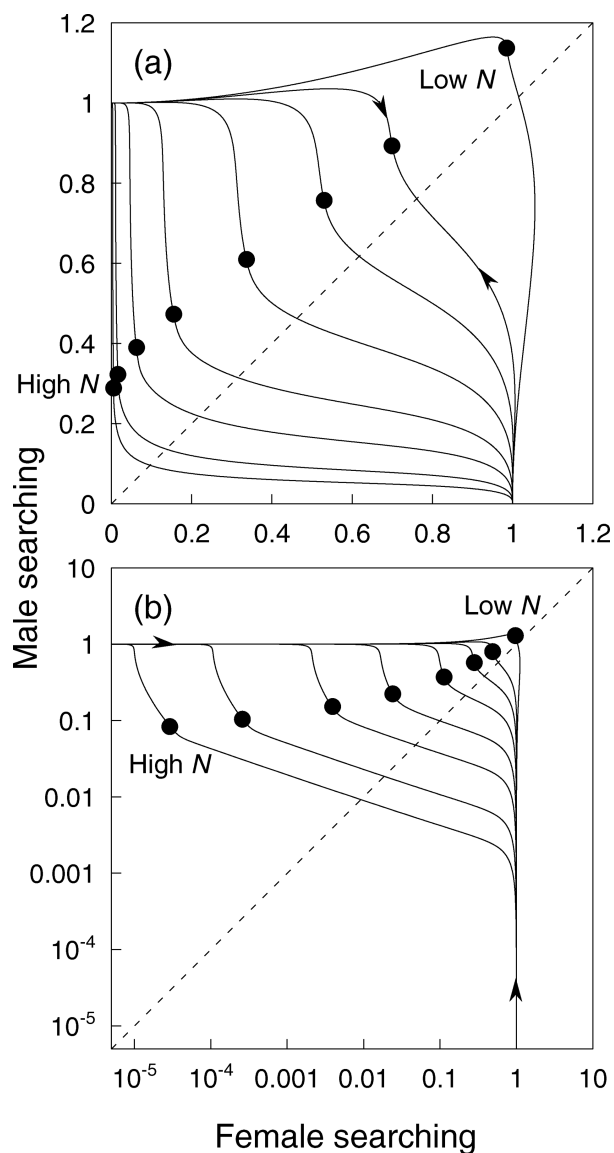

Figure 6. Evolutionary trajectories with sperm competition, when some activity is required from both sexes before mates can find each other: $f(x,y) = xy$. Other values as in Figure 5a, except that M takes values (from left to right) $M = 100, 50, 20, 10, 5, 3, 2, 1$, leading to $N = 13.1, 10.8, 7.6, 5.4, 3.6, 2.53, 1.93,$ and 1.28. In (a), the raw values of x and y are given, while in (b) investment in mate-searching is graphed as the proportional increase in mortality during time in caused by mate searching, $\mu_F(x)/\mu_F(0)$ and $\mu_M(y)/\mu_M(0)$. When mate-encounter rates are high to moderate, females pay extremely low costs for their searching (the "pheromone" case), whereas lowest mate-encounter rates may make both sexes increase their mortality by 100% or more (i.e., more than halve their survival).

Discussion

Recent theoretical literature has highlighted the need to reanalyze conflicts where reproductive activities can, in principle, be performed by either sex but, in reality, show strong sex biases. For example, female-biased parental care does not immediately follow from the fact that males can potentially reproduce more often than females. This is because actual (rather than potential) mating rates must be equal across the two sexes (e.g., Queller 1997; Kokko and Jennions 2003; Arnqvist 2004; Kokko et al. 2006), and models must take this into account to be self-consistent (Houston et al. 2005; Houston and McNamara 2005). This so-called Fisher condition (sensu Houston and McNamara 2005) has important consequences for mate searching. The intuitive reasoning, that males search because a high potential reproductive rate imposes high opportunity costs on them if they do not search, turns out to be fragile (Hammerstein and Parker 1987). If we assume that the production of offspring immediately follows every mating (i.e., no sperm competition), either sex can end up assuming the searching role, and males should be no more likely to take on the greater search effort than females even if the sexes differ in parental investment. The reason why the opportunity cost argument fails is that a male cannot mate if there are no females available to mate with, and the Fisher condition guarantees that males on average do not reproduce any faster than females. Instead, our results predict either divergence (the sex that ancestrally searched more ends up taking the searching role, that is, the "two ESS" solution found by Hammerstein and Parker 1987) or convergence, where both sexes search equally much. In either case, any notion that males should be automatically directed to the searching role merely because of differences in gametic investment remains unsupported.

Our models do, however, predict sexual asymmetries in two different ways. First, in the absence of multiple mating, a greater prevalence of male than female searching can be predicted if some aspect of female biology makes searching more costly for females than for males. We call this the *sex-specific cost hypothesis*. Second, when we allow for sperm competition in the model, an asymmetry is created that predicts much more mate searching by males. We call this the *multiple-mating hypothesis*. We consider each hypothesis in turn.

DOES THE UBIQUITY OF MALE SEARCHING REFLECT THE UBIQUITY OF SEX-SPECIFIC COSTS?

Sex differences in costs are probably common because males and females typically differ from each other in many aspects of their reproductive biology, and any differences such as size dimorphism or elaborate ornaments could cause the direct costs of searching (such as mortality) to differ between the sexes. Nevertheless, we consider it unlikely that sex-specific costs can explain the ubiquity of male searching in nature. For this hypothesis to generally favor male-mate searching, costs should be systematically higher for

females. It has been argued that this is the case when females already suffer high costs associated with some other aspect of reproduction. Greenfield (1981), for instance, suggested that mate searching by female moths would represent a considerable cost in addition to those already incurred from having to locate larval food resources for oviposition. Nevertheless, modeling shows that this intuitive argument can be surprisingly fragile.

The argument for why this should be the case requires considering both immediate and delayed costs of mate-searching effort, and we will first consider immediate costs. Our model assumes that mate searching increases mortality in either females or males for the duration of time that they search (i.e., once they mate, this immediate threat is removed). The model predicts an asymmetry in the search effort if this immediate increase in mortality is larger for one of the sexes, but this prediction is independent of any other life-history difference. If there is, for example, sexual size dimorphism, this may select for searching by the smaller sex if small individuals are better able to avoid predation while moving. But if predation is size-independent, then no sex difference is predicted despite the fact that the large and the small sex otherwise may follow different life histories (e.g., their vulnerability to starvation may differ). Thus, to evaluate if immediate costs support the role of the sex-specific hypothesis as an explanation of male-mate searching, one needs to estimate if mortality per unit of searching is larger for females. This is obviously challenging as differences in the actual mobility of the two sexes must be controlled for: instead of comparing current costs of searching, the question is how dangerous searching would be for one sex if it searched equally much as the other. One way to equalize mobility experimentally is to set it to zero: the use of immobile, man-made "model" animals (e.g., lizards made out of clay, Husak et al. 2006) can control for such biases but extrapolation will be required when applying such data to live, mobile individuals.

Keeping this caveat is mind, what is the evidence? Females may fall prey more easily in species with female-biased sexual size dimorphism (e.g., guppies *Poecilia reticulata*: Pocklington and Dill 1995) but, in general, we doubt that there is a general reason why mate searching should be more risky for females across all taxa. If anything, sexually selected males, because of their bright colors, conspicuous signals, and/or elaborate ornaments, are often argued to fall prey to predators more easily (Gwynne 1987; Götmark 1993; Acharya 1995; Koga et al. 2001; Stuart-Fox et al. 2003; Husak et al. 2006). Also note that opportunity costs and any sex-specific biases that are reflected in the OSR should not be included in costs of searching here: these are already accounted for by our model formulation through sex-specific time out values, yet they consistently fail to produce an asymmetry.

Immediate mortality costs of mate searching do not preclude other types of costs from occurring. Thus turning to the second question of delayed costs, it is possible that there are costs that

extend beyond the immediate mortality threat considered in our model. Mate searching typically not only consumes resources but also trades off with foraging, and both factors may compromise the condition of an individual and hence have a negative impact on its future reproductive success. Such costs are likely to affect the two sexes unequally. Female fitness is often limited by resources to make eggs, whereas male fitness is limited by numbers of mates. Thus females should be sensitive to costs of searching if these have an effect on fecundity, and males should be sensitive to costs of searching if these compromise his future mate acquisition ability. Neither type of delayed cost was included in our model, and the sex-specific hypothesis could therefore be resurrected as an explanation of male searching if there is clear evidence that males rarely face a trade-off between current and future reproductive effort (in the form of effort to acquire mates), whereas females commonly do so.

A direct comparison is again challenging, but a priori there is no reason to assume that males can perform mate acquisition "for free," nor is such a supposition supported by the literature. There is by now ample evidence for a trade-off between current and future reproduction in males (e.g., Badyaev and Qvarnström 2002; Hunt et al. 2004): they need resources to develop their sexual displays, and mate searching prevents foraging that is necessary to maintain condition and ensure future mate acquisition ability. Just how important this can be is evident in species in which only the males in best condition can mate at all: serious mate acquisition effort can be very delayed in such species (e.g., McDonald 1993; Owen-Smith 1993). When both male and female life histories are clearly shaped by delayed costs of current reproductive effort, a general statement that searching costs will be larger for females across various taxa would be definitely premature.

Despite our inability to assert that searching is generally costlier for females than for males, an examination of the empirical literature reveals some examples that appear to support the sex-specific cost hypothesis. In fiddler crabs *U. beebei*, for example, females search only when mate availability is high and plentiful burrows reduce sampling costs (deRivera et al. 2003). In California patch butterflies *Chlosyne californica*, easy searching in high-density conditions encourages males to abandon their regular "sit and wait" strategy to one of active search (Alcock 1994). Our model cannot explain such cases by varying multiple-mating opportunities through changes in mate-encounter rates. Instead, we expect these shifts to arise where variation in population density (or some other environmental factor that influences mate-encounter rates) covaries with mate-searching costs, while leaving mate-encounter rates relatively unchanged (meaning that female mating chances do not vary significantly with mate-encounter rates). The easiest imaginable situation is a case where densities vary but are always quite high, as in the fiddler crab example discussed earlier. Here, mate finding per se is not dif-

ficult for females, but sampling several males can be more costly than finding just one, and this cost may decrease with increasing density (see also deRivera 2005).

THE UBIQUITY OF MALE SEARCHING MOST LIKELY REFLECTS THE UBIQUITY OF MULTIPLE MATING

Our second explanation, the multiple-mating hypothesis, performs consistently better in predicting high searching effort for males and thus appears more robust in terms of correctly predicting the ubiquity of male searching in nature. It predicts an asymmetry in search effort despite the Fisher condition, that is, the fact that the number of offspring fathered by the male population must equal the number of offspring produced by females, which makes arguments based on high male potential reproductive rates nontrivial (Queller 1997; Kokko and Jennions 2003; Houston and McNamara 2005; Kokko et al. 2006). When there is multiple mating, the Fisher condition does not imply that individual females and males improve their fitness equally much by experiencing one more mating. In our model, another mating will not improve a female's reproductive output at all if she has already mated during the same mating window (Bateman 1948), but another mating by a male will always improve his chances of fathering offspring: thus $S_F \neq S_M$ is possible but only when at least some females mate multiply.

The multiple-mating hypothesis predicts a shift toward greater mate-searching effort by females when mate availability is low. Under these conditions females do not mate with very many males and may fail to find a mate quickly enough to optimize reproduction (Kokko and Mappes 2005). As densities increase, and females are no longer sperm limited, males alone are selected to compete for access to any unfertilized eggs that remain (for an empirical example see Levitan 2004).

The multiple-mating hypothesis additionally predicts cases in which females invest little in searching, but this small investment is very important for mate finding. This is seen, for example, in systems where members of one sex (usually females) produce pheromones to guide the mate searching efforts of the opposite sex (the "pheromone" case of Fig. 6). Such cases arise where mate finding is very difficult if one sex "does nothing." For example, deep sea hatchetfish *Argyropelecus hemigymnus* males attend to olfactory cues that are released by females to facilitate their search efforts (Jumper and Baird 1991). Once again, the effect of sperm competition appears capable of driving shifts in the amount of effort that a female must expend, even if female investment is quite low to begin with (evidence suggest that pheromones are relatively inexpensive to produce: Cardé and Baker 1984). At high density, for example, the need for female gypsy moths *Lymantria dispar* to invest any effort in pheromone emission is made redundant; competition among males is so intense that they will actively search out freshly emerged females even in the absence of any pheromone trails (Cardé and Hagaman 1984).

Both of our hypotheses predict possible phylogenetic inertia. One of the sexes can become "trapped" in a searching role if frequency dependence discourages searching in the sex that currently invests little in searching. This can maintain the original roles, even if the environment shifted to favor searching in the other sex. Phylogenetic analyses combined with information on population density could help distinguish between the two hypotheses: inertia should be weaker under the multiple mating than the sex-specific cost hypothesis, and when the inertia breaks, changes from male to female searching should occur in low-density conditions according to the multiple-mating hypothesis, but in high density according to the sex-specific cost hypothesis.

FURTHER POSSIBILITIES

In addition to the two different hypotheses discussed earlier, our models can be used to examine further alternative scenarios. An intriguing possibility is that the search function $f(x,y)$ itself is asymmetrical so that $\partial f/\partial x \neq \partial f/\partial y$ when $x = y$. Such an asymmetry should be rare, as there is no reason why a female that covers an extra distance of a given length, actively searching for a mate, should improve the meeting rate between the sexes any less than a male doing the same. Even pronounced differences in lifestyle, such as for example, flightlessness in some female insects, will not change this symmetry: these differences are reflected in other parts of the model such as vastly higher costs of moving for females, and should not be doubly accounted for by assuming a poor search outcome *if* the female moved instead of the male. However, an asymmetry in the actual search outcome $f(x,y)$ could arise, for example, if one of the sexes has better vision than the other: extreme examples are extra eyes of male mayflies (Kirschfeld and Wenk 1976) and bibionid flies (Zeil 1983). Such dimorphism would enhance any sex differences in selection pressures (mathematically, $\partial f/\partial y > \partial f/\partial x$). However, the extra eyes in these cases are believed to have evolved to enhance the pursuit of females and thus do not qualify as a preexisting trait that has led to males assuming the greater searching role.

Our model was designed to investigate the most basic form of mate searching, where potential mates do not differ in any direct or indirect benefits provided (nor is multiple mating assumed to be detrimental to either sex, but see Arnqvist and Rowe 2005). Although this assumption is a necessary first step in a general model of the evolution of mate-location traits, an obvious next step is to incorporate the possibility of mate sampling to improve mate quality (Byers et al. 2005; Dunn and Whittingham 2007), perhaps together with costs or benefits of multiple mating. This could potentially increase the prevalence of female searching if mate search improves mate quality, and provide an additional reason why sex-specific searching patterns can respond to density. For example, the prospects of finding a high-quality male may become worthwhile at high density where there are many males to choose from, whereas at low density such prospects might be too poor to pursue (Kokko and Rankin 2006). This could potentially help to explain why the mate-searching behaviors of, for example, the butterfly *C. pamphilus* (Wickman and Jansson 1997) and the California fiddler crab *U. crenulata* (deRivera 2005) appear to fit the sex-specific cost hypothesis better than the multiple-mating hypothesis. In the most complicated scenarios, females gain not only by choosing mates but also pay costs of mate sampling, both can vary with density, but changing female behavior with density implies that the prevalence of multiple mating varies too. Therefore, although the sex-specific cost and the multiple-mating hypothesis do not perform equally well when attempting to explain general patterns, they may have to be considered together (rather than as mutually exclusive alternatives) when considering specific cases.

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