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2007

Evolution Int J Org Evolution. 2007 May;61(5):1162-75.

http://hdl.handle.net/1975/5926
http://dx.doi.org/10.1111/j.1558-5646.2007.00090.x

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Evolution

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RRH: SEX ROLES IN MATE SEARCHING

WHAT DETERMINES SEX ROLES IN MATE SEARCHING?

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ABSTRACT

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 based on the ubiquity of sperm competition, and predicts that female searching can arise in low-density situations where 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, sex roles, sperm competition, multiple mating, pheromone

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 (for example 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. Since 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. Firstly, 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, while 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 has 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 suggest 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*, where 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 life time, 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, is 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, for example, colonial species). We begin by defining mate searching effort in a way that excludes non-adaptive 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 (versus 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 where 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, since 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 where 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 towards 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 (Figure 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.

186 'Time out' activities may involve parental care, replenishing sperm stores, or any other task
187 that must be performed before reproduction is possible again. Because sexes often differ
188 greatly in their parental investment, the duration of the time out period can be very different
189 for the sexes, which also limits their potential reproductive rate (PRR, Clutton-Brock and
190 Vincent 1991; Clutton-Brock and Parker 1992). For example, with mortality rate 0.1 and time
191 out $T_F = 1$ for females, females can reproduce, on average, approximately 10 times before
192 dying. By contrast, males with time out $T_M = 0.01$ can experience reproductive events at a
193 hundredfold rate compared to females during the same time frame (were they able to find the
194 necessary number of females with whom to mate; see Queller 1997; Kokko and Jennions
195 2003; Arnqvist 2004).

196 Female search effort, x, and male search effort, y, both influence the mating rate of females
197 and males who are in 'time in'. Females mate at a rate $m_F(x,y)$, and males at a rate $m_M(x,y)$.
198 These rates are increasing functions of both x and y. In a population with an unbiased
199 operational sex ratio (OSR), these two rates are equal. However, males and females can enjoy
200 different mating rates if the OSR is biased towards one or the other sex. In a population
201 consisting of β males : females in the 'time in' state, the mating rate for the two sexes can be
202 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
203 searching outcome, i.e. how mate encounter rates respond to mate-searching behavior of the
204 two sexes. Because searching improves mate encounter rates, we have $\partial f/\partial x > 0$, and $\partial f/\partial y >$
205 0, but many different functional forms are possible. For example, $f(x,y) = xy$ assumes that both
206 sexes must perform some searching before they can find each other at all, while $f(x,y)=x+y$
207 describes a species in which mates encounter each other frequently as soon as one of the sexes
208 searches sufficiently. The parameter M ($M > 0$) is used to compare mate encounter rates
209 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, $\beta = \beta(x,y)$, since 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, while 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 lifespan 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):

$$d\mathbf{v}/dt = \mathbf{vQ} \quad (1)$$

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

229
$$\mathbf{Q} = \left(q_{ij}\right) = \begin{pmatrix} -\frac{1}{T_{\mathrm{F}}} - \mu_{\mathrm{FO}} & m_{\mathrm{F}} & 0 & 0 \\ \frac{1}{T_{\mathrm{F}}} & m_{\mathrm{F}}(g-1) - \mu_{\mathrm{F}} & 0 & m_{\mathrm{M}} g \\ 0 & 0 & -\frac{1}{T_{\mathrm{M}}} - \mu_{\mathrm{MO}} & m_{\mathrm{M}} \\ 0 & m_{\mathrm{F}} g & \frac{1}{T_{\mathrm{M}}} & m_{\mathrm{M}}(g-1) - \mu_{\mathrm{M}} \end{pmatrix} \quad (2)$$

230 where, for brevity, we use notation m_{F} for $m_{\mathrm{F}}(x,y)$, μ_{F} for $\mu_{\mathrm{F}}(x)$, etc. The elements of this
231 matrix give the continuous-time *per capita* rates of changing from one state to another, where
232 the states are listed in the same order as in the vector **v** but now columns indicate the current
233 state and rows the future state. For example, column 1 lists two possible transitions made by a
234 female in the 'time out' state. She may return to 'time in', which happens at rate $1/T_{\mathrm{F}}$, and
235 since this means changing the reproductive value from v_{FO} to v_{FI} (i.e. add v_{FI}, remove v_{FO}), the
236 rate $1/T_{\mathrm{F}}$ appears as an addition in the 2nd column (the 2nd element gives v_{FI} in **v**) but as a
237 subtraction in the 1st row (corresponding to v_{FO} in **v**). The female may also die, which
238 happens at a rate μ_{FO}, and leads to a loss of reproductive value v_{FO} and no gain — i.e. the rate
239 μ_{FO} appears as an additional loss in row 1. Other columns are similarly derived. Reproduction
240 happens at rate m_{F} and m_{M} for females and males, respectively, and this adds reproductive
241 values of offspring g v_{FI} and g v_{MI} to the matrix equations. Note that offspring values do not
242 depend on who the parents were, thus we ignore the possibility that mate searching evolves as
243 a means to sample several potential mates and mate with the ones of highest quality; see
244 Discussion for this limitation.

245 Härdling et al. (2003) produced a method to calculate the selection differentials in a
246 continuous-time setting with several states. When a resident population (using x^*, y^*) is at
247 population equilibrium, the reproductive values $\mathbf{v}^*$ satisfy $\mathrm{d}\mathbf{v}^*/\mathrm{d}t = 0$ (Härdling et al. 2003).

The equilibrium requirement yields the following relationships between reproductive values of states:

$$v_{FI}^*/v_{FO}^* = 1+\mu_{FO}T_F \tag{3a}$$

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

and

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

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,

$$S_{\mathrm{F}} = g\frac{1}{m_{\mathrm{F}}}\frac{\partial m_{\mathrm{F}}}{\partial x} - \frac{1}{\mu_{\mathrm{F}}}\frac{\mathrm{d}\mu_{\mathrm{F}}}{\mathrm{d}x} \quad (5a)$$

A similar derivation gives the male selection differential

$$S_{\mathrm{M}} = g\frac{1}{m_{\mathrm{M}}}\frac{\partial m_{\mathrm{M}}}{\partial y} - \frac{1}{\mu_{\mathrm{M}}}\frac{\mathrm{d}\mu_{\mathrm{M}}}{\mathrm{d}y} \quad (5b)$$

The conditions $S_{\mathrm{F}} > 0$ and $S_{\mathrm{M}} > 0$ 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: while it influences m_{F} and m_{M}, it cancels out in the LHS of eqs. 5a-b.

How should the independence of searching roles from reproductive effort (time out) be understood? The term $1/m_{\mathrm{F}}\ \partial m_{\mathrm{F}}/\partial x$ 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 $1/m_{\mathrm{M}}\ \partial m_{\mathrm{M}}/\partial y$. Since 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 (Figure 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 (Figure 2a), accelerating (quadratic; Figure 2b) or strongly accelerating (Figure 2c). In the first case, we predict that only one sex searches, and initial, incidental factors determine which one it is (Figure 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 towards a single equilibrium, where they invest equal effort into mate searching (Figure 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 to males, shifts the basins of attraction from a symmetrical case (Figure 3a) to one where evolution more easily proceeds towards male searching (Figure 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*, for example, typically mate once and then spend the rest of their lives looking for

335 places to lay their eggs: Gotthard et al. 1999), in many species females often mate multiply
336 before any offspring are produced (Jennions and Petrie 2000). This introduces sperm
337 competition, and means that some (often many) matings do not lead to fertilization.

338 We now introduce a biologically determined minimum time spent in mating activities — the
339 mating window. For our argument it does not matter if it is asynchronous or synchronous
340 between females; in the model it is kept asynchronous. The mating window is included in
341 'time in', and females spend it acquiring multiple matings. Offspring can be sired by any male
342 who mates with the female during the mating window. The duration of the mating window
343 can be arbitrarily defined (we use unity). The duration can be short: for example in frogs, the
344 mating window for a female could be simply the time it takes to release all of her eggs.
345 During this time, several males may be trying to amplex the female, resulting in multiple
346 matings (Byrne and Roberts 2000). In a seasonally breeding organism that can store sperm, on
347 the other hand, the mating window can be a whole year, if a female lays eggs in the spring and
348 uses sperm from males she has encountered up to a year before. Nevertheless, she may not
349 have encountered many males, if the mate encounter rate M during this year has been small
350 (e.g. a result of infrequent, perhaps once-a-year nuptial flights).

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

Since 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 (equation 5a), up to a proportionality constant, now takes the form

$$S_F = g\frac{1}{p}\frac{\partial p}{\partial x} - \frac{1}{\mu_F}\frac{\partial \mu_F}{\partial x}$$

$$= b_F\frac{\partial m_F}{\partial x} - \frac{1}{\mu_F}\frac{\partial \mu_F}{\partial x}, \text{ where } b_F = g\frac{e^{-N}}{1-e^{-N}} \quad (6)$$

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,

379 $$\sum_{i=0}^{\infty} \frac{g}{i+1} e^{-N} \left(\frac{N^i}{i!} \right) = g \frac{1-e^{-N}}{N} \quad (7a)$$

380 which gives the male selection differential

381 $$S_{\mathrm{M}} = b_{\mathrm{M}} \frac{\partial m_{\mathrm{M}}}{\partial y} - \frac{1}{\mu_{\mathrm{M}}} \frac{\partial \mu_{\mathrm{M}}}{\partial y}, \text{ where } b_{\mathrm{M}} = g \frac{1-e^{-N}}{m_{\mathrm{M}} N} \quad (7b)$$

382 The terms b_{F} and b_{M} relate mating success to offspring production, i.e. they are the slopes of
383 the Bateman gradient (Bateman 1948). The ratio $b_{\mathrm{M}}/b_{\mathrm{F}}$, describing how much more males
384 benefit from finding additional mates than females, increases very strongly with multiple
385 mating (Figure 4). When one mating window offers an abundance of mating opportunities,
386 most matings are superfluous to females: they do not make a difference to whether she can
387 commence reproduction or not, leading to a shallow slope $\partial p/\partial x$ and therefore a small b_{F}. For
388 males, each mating also brings about smaller expected fitness gains when there is much sperm
389 competition (b_{M} decreases with N), but every mating, nevertheless, contributes to additional
390 paternity chances; b_{M} therefore stays above b_{F}, the difference increasing with N (Figure 4).

391 *Sperm competition: results*

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

399 males and females (dots near the right end of Figure 5a). More intensive mate searching
400 does not fully compensate for the rarity of mate encounters, as *N* stays low at this end of
401 Figure 5a.

402 It is notable that the same outcomes are approached, regardless of whether females or males
403 were assumed to be the originally searching sex (Figure 5a). In other words, including sperm
404 competition reduces the tendency for sex roles to be divergent (Figure 4 and 5a). However, if
405 costs have a similar shape that produced divergent roles in the model without sperm
406 competition — i.e. little acceleration and thus little 'extra' cost for the already searching sex
407 to search more — and if the mate encounter rate *M* is low, then divergence can be found even
408 when sperm competition is included (Figure 5b). Females are not very likely to find several
409 males during one mating window when *M* is low, which explains its resemblance to the
410 scenario without sperm competition. For example, the lowest value of *M* considered in Figure
411 5b ($M = 0.1$) will retain female searching at equilibrium if they were initially the searching
412 sex. At this equilibrium, $N = 0.37$, such that females will not find a male in $\exp(-0.37) = 69\%$
413 of all their attempts to complete a mating window, and only 5% of females mate multiply.

414 The model can also be applied to cases where mate location is extremely difficult unless both
415 sexes indicate their presence in some way to members of the opposite sex. This is seen, for
416 example, in many insect systems where mate-finding is mediated by pheromones produced by
417 females to attract mate-searching males. In some extreme cases, sex differences in mobility
418 (e.g. ability to fly) mean that females are entirely dependent on searching males who detect
419 and locate the "calling" females (Alcock 1981). There may often be remarkable asymmetry in
420 the effort expended by each sex. Females often only need to release minute quantities of
421 pheromone to elicit a strong response from patrolling males. The cost of pheromone
422 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 Figure 6b). Males, in the meanwhile, accept much higher costs. However, if an average female finds less than 4 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, Figure 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.

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, i.e. 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

494 two sexes must be controlled for: instead of comparing current costs of searching, the
495 question is how dangerous searching would be for one sex if it searched equally much as the
496 other. One way to equalize mobility experimentally is to set it to zero: the use of immobile,
497 man-made 'model' animals (e.g. lizards made out of clay, Husak et al. 2006) can control for
498 such biases but extrapolation will be required when applying such data to live, mobile
499 individuals.

500 Keeping this caveat is mind, what is the evidence? Females may fall prey more easily in
501 species with female-biased sexual size dimorphism (e.g. guppies *Poecilia reticulata*:
502 Pocklington and Dill 1995) but, in general, we doubt that there is a general reason why mate
503 searching should be more risky for females across all taxa. If anything, sexually-selected
504 males, because of their bright colors, conspicuous signals, and/or elaborate ornaments, are
505 often argued to fall prey to predators more easily (Gwynne 1987; Götmark 1993; Acharya
506 1995; Koga et al. 2001; Stuart-Fox et al. 2003; Husak et al. 2006). Also note that opportunity
507 costs and any sex-specific biases that are reflected in the OSR should not be included in costs
508 of searching here: these are already accounted for by our model formulation through sex-
509 specific 'time out' values, yet they consistently fail to produce an asymmetry.

510 Immediate mortality costs of mate searching do not preclude other types of costs from
511 occurring. Thus turning to the second question of delayed costs, it is possible that there are
512 costs that extend beyond the immediate mortality threat considered in our model. Mate-
513 searching typically not only consumes resources but also trades off with foraging, and both
514 factors may compromise the condition of an individual and hence have a negative impact on
515 its future reproductive success. Such costs are likely to affect the two sexes unequally. Female
516 fitness is often limited by resources to make eggs, while male fitness is limited by numbers of
517 mates. Thus females should be sensitive to costs of searching if these have an effect on

518 fecundity, and males should be sensitive to costs of searching if these compromise his
519 future mate acquisition ability. Neither type of delayed cost was included in our model, and
520 the sex-specific hypothesis could therefore be resurrected as an explanation of male searching
521 if there is clear evidence that males rarely face a trade-off between current and future
522 reproductive effort (in the form of effort to acquire mates) while females commonly do so.

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

534 Despite our inability to assert that searching is generally costlier for females than for males,
535 an examination of the empirical literature reveals some examples that appear to support the
536 sex-specific cost hypothesis. In fiddler crabs *Uca beebei*, for example, females search only
537 when mate availability is high and plentiful burrows reduce sampling costs (deRivera et al.
538 2003). In California patch butterflies *Chlosyne californica*, easy searching in high density
539 conditions encourages males to abandon their regular 'sit and wait' strategy to one of active
540 search (Alcock 1994). Our model cannot explain such cases by varying multiple mating
541 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 above. Here, mate finding per se is not difficult 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, i.e. 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 non-trivial (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 towards 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

566 Mappes 2005). As densities increase, and females are no longer sperm limited, males alone
567 are selected to compete for access to any unfertilized eggs that remain (for an empirical
568 example see Levitan 2004).

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

583 Both of our hypotheses predict possible phylogenetic inertia. One of the sexes can become
584 'trapped' in a searching role if frequency dependence discourages searching in the sex that
585 currently invests little in searching. This can maintain the original roles, even if the
586 environment shifted to favor searching in the other sex. Phylogenetic analyses combined with
587 information on population density could help distinguish between the two hypotheses: inertia
588 should be weaker under the multiple mating than the sex-specific cost hypothesis, and when
589 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 above, 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 e.g. 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 pre-existing 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). While 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, while 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 *Coenonympha pamphilus* (Wickman and Jansson 1997) and the California fiddler crab *Uca crenulata* (deRivera 2005) appear to fit the sex-specific cost hypothesis better than the multiple mating hypothesis. In the most complicated scenarios, females gain 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, while 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.

ACKNOWLEDGEMENTS

We thank M. Jennions, L. Rowe and an anonymous reviewer for their constructive comments, as well as P. Backwell and G. Parker for inspiring and helpful discussions. Funding was provided by the Academy of Finland (to HK and BBMW), the Australian Research Council (to BBMW), and the Centre for International Mobility (to BBMW).

LITERATURE CITED

Acharya, L. 1995. Sex-biased predation on moths by insectivorous bats. Anim. Behav. 49: 1461-1468.

637 Alcock, J. 1981. Notes on the reproductive behaviour of some Australian thynnine wasps
638 (Hymenoptera: Tiphiidae). J. Kansas Entomol. Soc. 54: 681-693.

639 Alcock, J. 1994. Alternative mate-locating tactics in *Chlosyne californica* (Lepidoptera,
640 Nymphalidae). Ethology 97:103-118.

641 Alexander, R. D. 1975. Natural selection and specialized chorusing behaviour in acoustical
642 insects. Pages 35-77 *in* D. Pimentel, ed. *Insects, Science and Society*. Academic Press,
643 New York.

644 Angioy, A. M., A. Desogus, I. T. Barbarossa, P. Anderson, and B. S. Hansson. 2003. Extreme
645 sensitivity in an olfactory system. Chem. Senses 28:279-284.

646 Arnqvist, G. 2004. Sexual conflict and sexual selection: Lost in the chase. Evolution 58:1383-
647 1388.

648 Arnqvist, G., and L. Rowe. 2005. Sexual conflict. Princeton University Press, Princeton.

649 Badyaev, A.V., and A. Qvarnström, A. 2002. Putting sexual traits into the context of an
650 organism: a life-history perspective in studies of sexual selection. Auk 119:301-310.

651 Bateman, A.J. 1948. Intrasexual selection in Drosophila. Heredity 2:349-368.

652 Blows, M. W. 2002. Interaction between natural and sexual selection during the evolution of
653 mate recognition. Proc. Roy. Soc. Lond. B 269: 1113-1118.

654 Byers, J.A., P.A. Wiseman, L. Jones, and T.J. Roffe. 2005. A large cost of female mate
655 sampling in pronghorn. Am. Nat. 166:661-668.

656 Byrne, P.G., and J. D. Roberts. 2000. Does multiple paternity improve the fitness of the frog
657 *Crinia georgiana*? Evolution 54:968-973.

658 Byrne, P.G., and J. D. Roberts. 2004. Intrasexual selection and group spawning in quacking
659 frogs (*Crinia georgiana*). Behav. Ecol. 15:872-882.

660 Cardé, R. T., and T. C. Baker. 1984. Sexual communication with pheromones. Pages 355-383
661 *in* W. J. Bell, and R. T. Cardé, ed. *Chemical ecology of insects*. Chapman & Hall, New
662 York.

663 Cardé, R. T., and T. E. Hagaman. 1984. Mate location strategies of gypsy moths in dense
664 populations. J. Chemical Ecol. 10: 25-31.

Clutton-Brock, T. H., and G. A. Parker. 1992. Potential reproductive rates and the operation of sexual selection. Q. Rev. Biol. 67:437-456.

Clutton-Brock, T. H., and A. C. J. Vincent. 1991. Sexual selection and the potential reproductive rates of males and females. Nature 351:58-60.

Davies, N. B., and T. R. Halliday. 1979. Competitive mate searching in common toads, *Bufo bufo*. Anim. Behav. 27: 1253-1267.

deRivera, C. E. 2005. Long searches for male-defended breeding burrows allow female fiddler crabs, *Uca crenulata*, to release larvae on time. Anim. Behav. 70: 289-297.

deRivera, C. E., P. R. Y. Backwell, J. H. Christy, and S. L. Vehrencamp. 2003. Density affects female and male mate searching in the fiddler crab, *Uca beebei*. Behav. Ecol. Sociobiol. 53: 72-83.

Dunn, P.O., and L.A. Whittingham. 2007. Search costs influence the spatial distribution, but not the level, of extra-pair mating in tree swallows. Behav. Ecol. Sociobiol. 61:449-454.

Götmark, F. 1993 Conspicuous coloration in male birds is favoured by predation in some species and disfavoured in others. Proc. Roy. Soc. Lond. B 253: 143-146.

Gotthard, K., S. Nylin, and C. Wicklund. 1999. Mating system evolution in response to search costs in the speckled wood butterfly, *Pararge aegeria*. Behav. Ecol. Sociobiol. 45: 424-429.

Grafe, T. U. 1997. Costs and benefits of mate choice in the lek-breeding reed frog, *Hyperolius marmoratus*. Anim. Behav. 53: 1103-1117.

Greenfield, M. D. 1981. Moth sex pheromones: an evolutionary perspective. Florida Entomol. 64:4-17.

Groddeck, J., V. Mauss, and K. Reinhold. 2004. The resource-based mating system of the Mediterranean pollen wasp *Ceramius fonscolombei* Latreille 1810 (Hymenoptera, Vespidae, Masarinae). J. Insect Behav. 17: 397-418.

Gwynne, D. T. 1987. Sex-biased predation and the risky mate-locating behaviour of male tick-tock cicadas (Homoptera: Cicadidae). Anim. Behav. 35: 571-576.

Hammerstein, P., and G. A. Parker. 1987. Sexual selection: Games between the sexes. Pages 119-142 *in* J. W. Bradbury, and M. B. Andersson, ed. *Sexual selection: Testing the alternatives*. Wiley, Chichester.

695 Härdling, R., and A. Kaitala. 2005. The evolution of repeated mating under sexual conflict.
696 J. Evol. Biol. 18:106-115.

697 Härdling, R., H. Kokko, and K. E. Arnold. 2003. Dynamics of the caring family. Am. Nat.
698 161: 395-412.

699 Houston, A. I., and J. M. McNamara. 2002. A self-consistent approach to paternity and
700 parental effort. Phil. Trans. Roy. Soc. Lond. B 357:351-362.

701 Houston, A.I., and J. M. McNamara. 2005. John Maynard Smith and the importance of
702 consistency in evolutionary game theory. Biol. & Philos. 20:933-950.

703 Houston, A.I., T. Székely, and J. M. McNamara. 2005. Conflict between parents over care.
704 Trends Ecol. Evol. 20:33-38.

705 Hunt, J., R. Brooks, M.D. Jennions, M.J. Smith, C.L. Bentsen, & L.F. Bussière. 2004. High-
706 quality male field crickets invest heavily in sexual display but die young. Nature
707 432:1024-1027.

708 Husak, J.F., J.M. Macedonia, S.F. Fox, and R.C. Sauceda. 2006. Predation cost of
709 conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental
710 test using clay-covered model lizards. Ethology 112:572-580.

711 Ide, J.-Y., and M. Kondoh, 2000. Male-female evolutionary game on mate-locating behaviour
712 and evolution of mating systems in insects. Ecol. Lett. 3:433-440.

713 Jennions, M. D., and M. Petrie. 2000. Why do females mate mutiply? A review of the genetic
714 benefits. Biol. Rev. 75:21-64.

715 Jumper, G. Y. Jr., and R. C. Baird. 1991. Location by olfaction: a model and application to
716 the mating problem in the deep-sea hatchetfish *Argyropelecus hemigymnus*. Am. Nat.
717 138:1431-1458.

718 Kasumovic, M.M., M.J. Bruce, M.E. Herberstein, and M.C.B. Andrade. 2007. Risky mate
719 search and mate preference in the golden orb-web spider (*Nephila plumipes*). Behav.
720 Ecol. 18:189-195.

721 Kirschfeld, K., and P. Wenk. 1976. The dorsal compound eye of simuliid flies: an eye
722 specialized for the detection of small, rapidly moving objects. Z. Naturforschung
723 31:764-765.

724 Koga, T., P. R. Y. Backwell, J. H. Christy, M. Murai, and E. Kasuya. 2001. Male-biased
725 predation of a fiddler crab. Anim. Behav. 62: 201-207.

726 Kokko, H., M. D. Jennions, and R. Brooks. 2006. Unifying and testing models of sexual
727 selection. Ann. Rev. Ecol. Evol. Syst. 37:43-66.

728 Kokko, H., and M. D. Jennions. 2003. It takes two to tango. Trends Ecol. Evol. 18:103-104.

729 Kokko, H., and J. Mappes. 2005. Sexual selection when fertilization is not guaranteed.
730 Evolution 59:1876-1885.

731 Kokko, H., and P. Monaghan. 2001. Predicting the direction of sexual selection. Ecol. Lett.
732 4:159-165.

733 Kokko, H., and I. Ots. 2006. When not to avoid inbreeding. Evolution 60:467-475.

734 Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? Density-dependent
735 effects in mating systems. Phil. Trans. Roy. Soc. Lond. B 361:319-334.

736 Kuussaari, M., I. Saccheri, M. Camara, and I. Hanski. 1998. Allee effect and population
737 dynamics in the Glanville fritillary butterfly. Oikos 82:384-392.

738 Levitan, D.R. 2004. Density-dependent sexual selection in external fertilizers: Variances in
739 male and female fertilization success along the continuum from sperm limitation to
740 sexual conflict in the sea urchin *Strongylocentrotus franciscanus.* Am. Nat. 164: 298-
741 309.

742 Lucas, J.R., and R.D. Howard. 1995. On alternative reproductive tactics in anurans: Dynamic
743 games with density and frequency dependence. Am. Nat. 146:365-397.

744 McDonald, D.B. 1993. Demographic consequences of sexual selection in the long-tailed
745 manakin. Behav. Ecol. 4:297-309.

746 McNamara, J.M., and A.I. Houston. 1986. The common currency for behavioural decisions.
747 Am. Nat. 127:358-378.

748 McNamara, J.M., and A.I. Houston. 1996. State-dependent life histories. Nature 380:215-221.

749 Melville, J. M., S. K. Tallarovic, and P. H. Brownell. 2003. Evidence of mate trailing in the
750 giant hairy desert scorpion, *Hadrurus arizonensis*. J. Insect Behav. 16: 97-115.

751 Metz, J.A.J., R. M. Nisbet, and S.A.H. Geritz. 1992. How should we define ‘fitness’ for
752 general ecological scenarios? Trends Ecol. Evol. 7:198-202.

753 Nahrung, H. F., and G. A. Allen. 2004. Sexual selection under scramble competition: mate
754 location and mate choice in the Eucalypt leaf beetle *Chrysophtharta agricola* (Chapuis)
755 in the field. J. Insect Behav. 17: 353-366.

756 Okuda, N. 1999. Female mating strategy and male brood cannibalism in a sand-dwelling
757 cardinalfish. Anim. Behav. 58: 273-279.

758 Owen-Smith, N. 1993. Age, size, dominance and reproduction among male kudus: mating
759 enhancement by attrition of rivals. Behav. Ecol. Sociobiol. 32:177-184.

760 Parker, G.A. 1978. Searching for mates. Pages 214-244 *in* J. R. Krebs, and N. B. Davies, ed.
761 *Behavioural ecology: an evolutionary approach*. Blackwell Press, London.

762 Parker, G. A., and L. W. Simmons. 1996. Parental investment and the control of sexual
763 selection: predicting the direction of sexual competition. Proc. Roy. Soc. Lond. B
764 263:315-321.

765 Pen, I., F.J. Weissing, and S. Daan. 1999. Seasonal sex ratio trend in the European Kestrel: an
766 evolutionarily stable strategy analysis. Am. Nat. 153:384-397.

767 Pocklington, R., and L. M. Dill. 1995. Predation on females or males: who pays for bright
768 male traits? Anim. Behav. 49: 1122-1124.

769 Queller, D. C. 1997. Why do females care more than males? Proc. Roy. Soc. Lond. B
770 264:1555-1557.

771 Rhainds, M., G. Gries, and M. M. Min. 1999. Size- and density-dependent reproductive
772 success of bagworms, *Metisa plana*. Entomol. Exp. Appl. 91:375-383.

773 Stuart-Fox, D.M., A. Moussalli, N. J. Marshall, and I. P. F. Owens. 2003. Conspicuous males
774 suffer higher predation risk: visual modelling and experimental evidence from lizards.
775 Anim. Behav. 66: 541-550.

776 Svensson, M. 1996. Sexual selection in moths: The role of chemical communication. Biol.
777 Rev. 71:113-135.

778 Takàcs, S., G. Gries, and R. Gries. 2002. Where to find a mate? Resource-based sexual
779 communication of webbing clothes moth. Naturwissenschaften 89: 57-59.

780 Taylor, P.D. 1990. Allele-frequency change in a class-structured population. Am. Nat.
781 135:95-106.

782 Trivers, R. 1972. Parental investment and sexual selection. Pages 139-179 *in* B. Campbell,
783 ed. *Sexual selection and the descent of man 1871-1971*. Aldine Press, Chicago.

784 Webb, J. N., A. I. Houston, J. M. McNamara, and T. Székely. 1999. Multiple patterns of
785 parental care. Anim. Behav. 58:983-993.

786 Wells, K. D. 1977. The social behaviour of anuran amphibians. Anim. Behav. 25:666-693.

787 Wickman, P.-O., and P. Jansson. 1997. An estimate of female mate searching costs in the
788 lekking butterfly *Coenonympha pamphilis*. Behav. Ecol. Sociobiol. 40:321-328.

789 Wickman, P.-O., and R. L. Rutowski. 1999. The evolution of mating dispersion in insects.
790 Oikos 84:463-472.

791 Wiklund, C., A. Kaitala, and N. Wedell. 1998. Decoupling of reproductive rates and parental
792 expenditure in a polyandrous butterfly. Behav. Ecol. 9:20-25.

793 Zeil, J. 1983. Sexual dimorphism in the visual system of flies: the compound eyes and neural
794 superposition in Bibionidae (Diptera). J. Comp. Physiol. 150:379-393.

FIGURE LEGENDS

Fig. 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.

Fig. 2 Evolutionary trajectories without sperm competition, when evolutionary change per generation is proportional to the LHS of eqs. 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: $T_F = 1$, $T_M = 0.01$, $M = 1$ (though these parameters do not influence solutions as long as there is no sperm competition, see eqs. 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 $\mu_M(y) = 0.1\ (1+y^{2.5})$.

Fig. 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 non-linear 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 $\mu_M(y) = 0.1\ (1+y^{1.2})$.

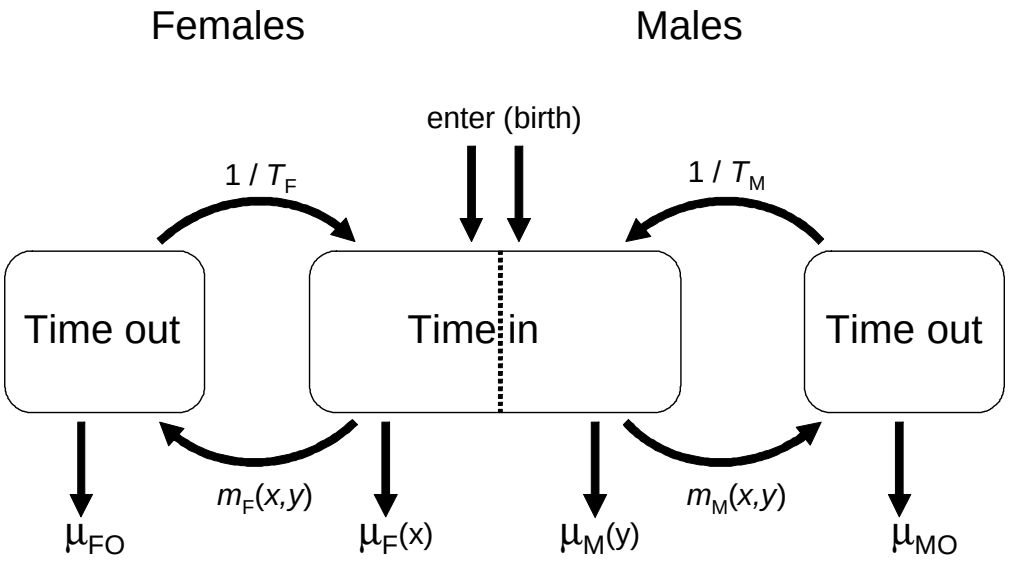
Fig. 4 The Bateman gradients, i.e. the reproductive benefits b_M and b_F for female and males, respectively, from improved mate encounter rates, and the ratio b_M/b_F, for

different values of the average number of matings per mating window, N. The decrease 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.

Fig. 5 Evolutionary trajectories with sperm competition. Solutions 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 equilibrium 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).

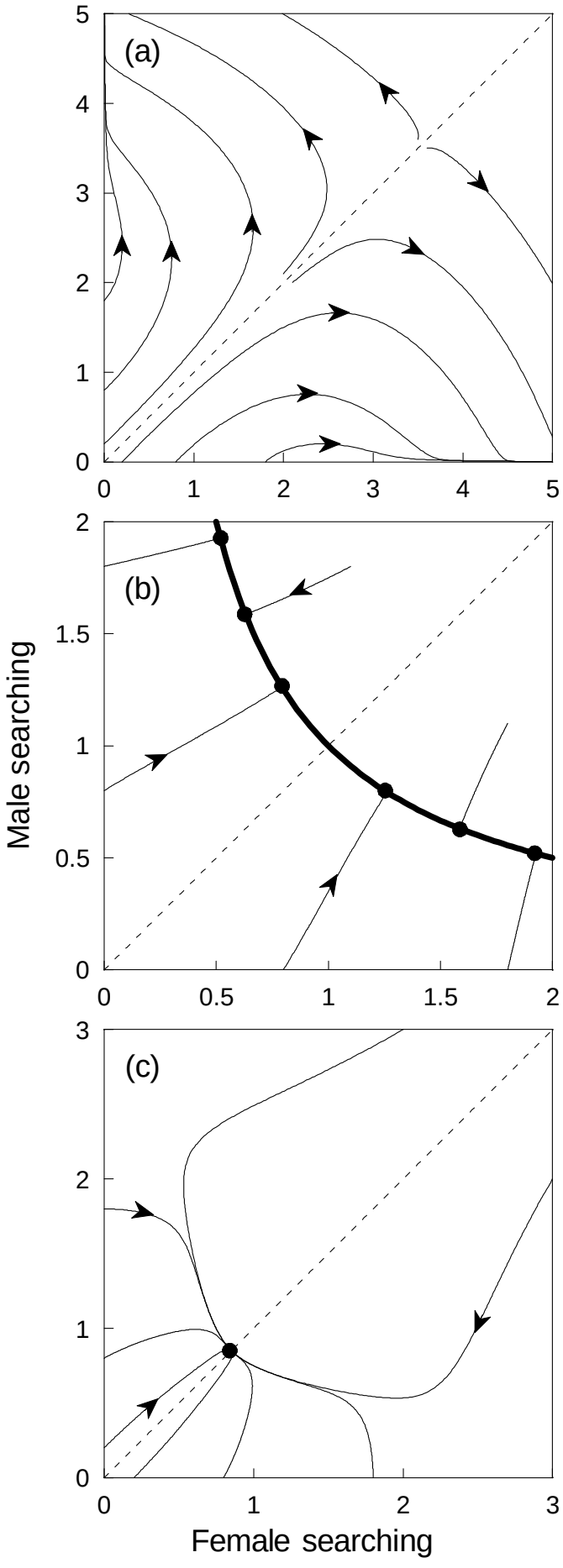
Fig. 6 Evolutionary trajectories with sperm competition, when some activity is required from both sexes before mates can find each other: $f(x,y) = xy$. Other values as in Figure 5a, except that M takes values (from left to right) M = 100, 50, 20, 10, 5, 3, 2, 1, leading to N = 13.1, 10.8, 7.6, 5.4, 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), while lowest mate encounter rates may make both sexes increase their mortality by 100% or more (i.e. more than halve their survival).


Females
Males
enter (birth)
1 / T_F
1 / T_M
Time out
Time in
Time out
$m_F(x,y)$
$m_M(x,y)$
μ_{FO}
$\mu_F(x)$
$\mu_M(y)$
μ_{MO}

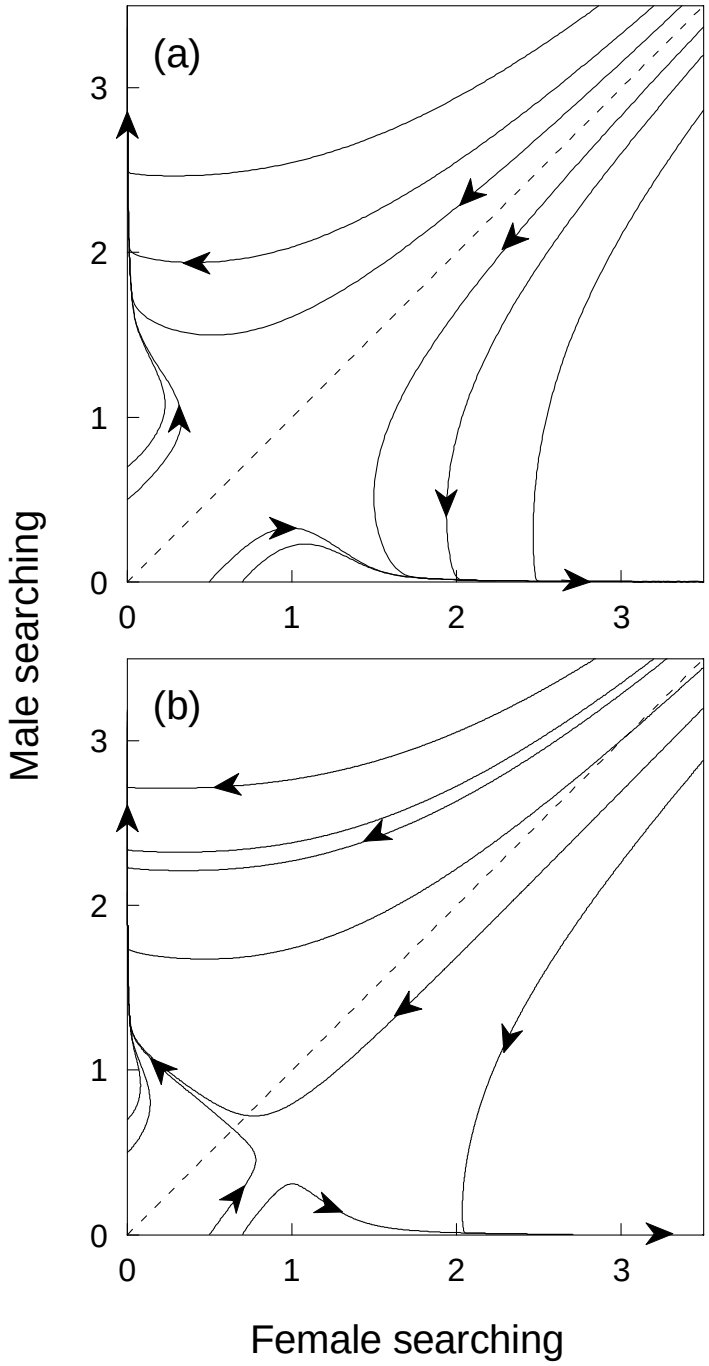
847

848 Fig. 1.



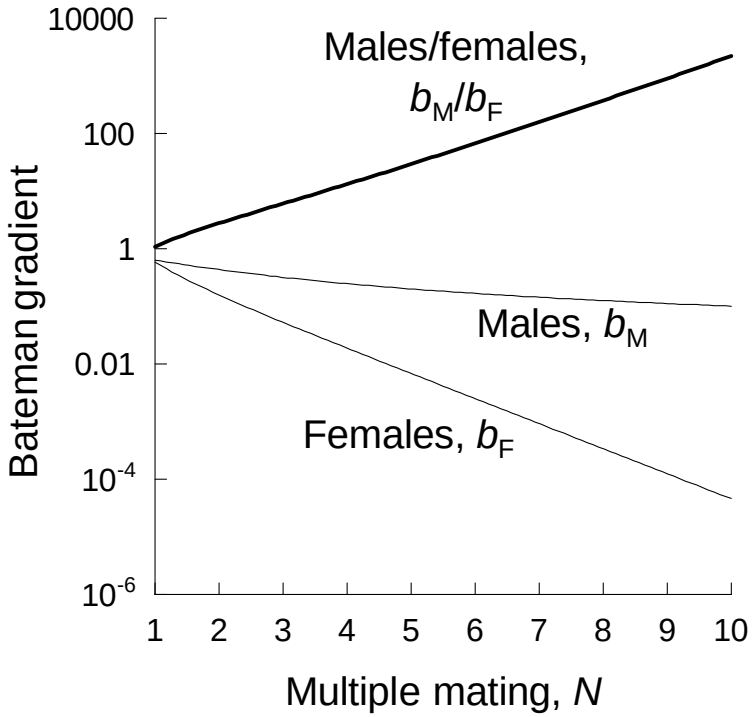
849

Fig. 2



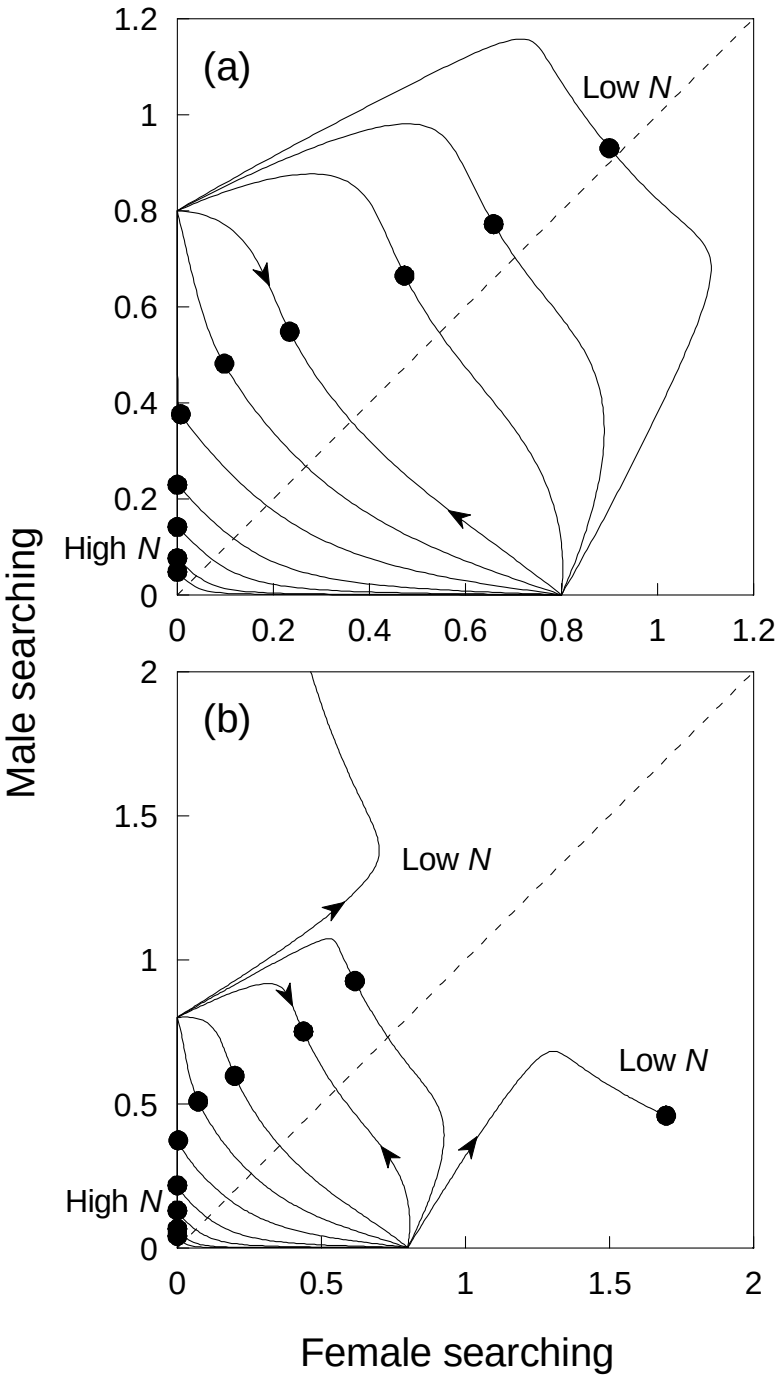
850

Fig. 3


10000
100
1
0.01
10^{-4}
10^{-6}
Bateman gradient
Males/females,
b_M/b_F
Males, b_M
Females, b_F
1 2 3 4 5 6 7 8 9 10
Multiple mating, N

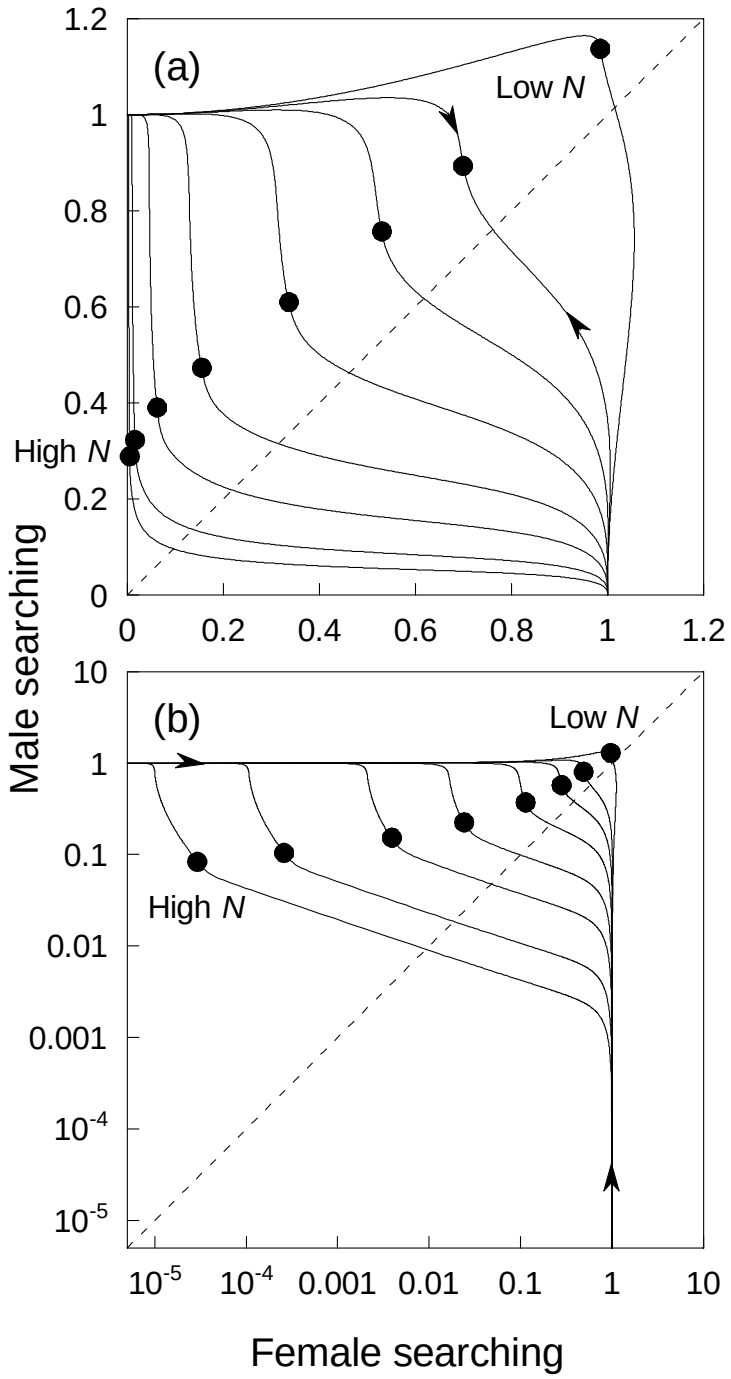
851

852 Fig. 4


(a)
Low N
High N
(b)
Low N
Low N
High N
Male searching
Female searching
0
0.2
0.4
0.6
0.8
1
1.2
0.5
1.5
2

853

Fig. 5


(a)
Low N
High N
1.2
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1
1.2
(b)
Low N
High N
10
1
0.1
0.01
0.001
10-4
10-5
10-5
10-4
0.001
0.01
0.1
1
10
Male searching
Female searching

854 Fig. 6

855