

1 **Evolution**

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3 RRH: SEX ROLES IN MATE SEARCHING

4 WHAT DETERMINES SEX ROLES IN MATE SEARCHING?

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## ABSTRACT

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

41 **Key words:** mate search, sex roles, sperm competition, multiple mating, pheromone

42 In most sexually reproducing organisms, finding a conspecific mate requires some form of  
43 physical activity: at least the gametes, but often the organisms themselves, have to be mobile.  
44 Effort invested into mate searching, however, can be costly (Gwynne 1987; Acharya 1995;  
45 Grafe 1997; Okuda 1999; Melville et al. 2003; Kasumovic et al. 2007). Searching effort can  
46 be defined as a costly activity that evolves to improve mate encounter rates, whether this  
47 involves physical movement or some other form of active behavior (for example calls or  
48 pheromone production). For individuals of one sex, the problem is solved — in the sense that  
49 mate finding does not require any effort — if the opposite sex performs sufficient searching.  
50 Since males of a typical species benefit from multiple mating more than females (Bateman  
51 1948), they are typically expected to be the mate-searching sex, and females should  
52 consequently spend zero effort in mate-searching.

53 There are two reasons, however, why mate searching deserves closer attention: one  
54 theoretical, and one empirical. Firstly, we lack a general theoretical explanation for the fact  
55 that males often take on the searching role. In a seminal paper, Hammerstein and Parker  
56 (1987) considered the mate search conundrum using a game theoretical approach. Their  
57 ‘mobility game’ attempted to explain why one sex should invest greater search and movement  
58 effort than the other, and why males tend to be the ones that end up assuming the greater  
59 effort (i.e. females typically ‘win’ the game). Prima facie, one might expect males to be the  
60 more mobile sex if females invest more in offspring and represent a limiting resource for  
61 males (Parker 1978). Hammerstein and Parker (1987) found, however, that a searching male  
62 strategy and a searching female strategy were alternative evolutionary stable strategies  
63 (ESSs). The relative investment in offspring did not matter to the model outcome, and females  
64 could ‘lose’ both the game over parental investment and the one over effort spent in  
65 searching.

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

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

90 On the other hand, evidence from other taxa suggests that high density can favor male, rather  
91 than female, searching (Kokko and Rankin 2006). In several species of frogs and orthoptera,  
92 for example, males, at low densities, use acoustic signals to attract searching females but, at  
93 higher densities, may switch over to a roaming strategy (Alexander 1975; Wells 1977; Davies  
94 and Halliday 1979; Byrne and Roberts 2004). Although one should keep in mind taxon-  
95 specific explanations, such as the need to avoid male-male competition caused by silent  
96 satellite frogs that join calling males (Lucas and Howard 1995), this alternative response to  
97 density has also led to a suggested general explanation of sex roles (Wickman and Rutowski  
98 1999): males should be the default searching sex because they have the most to gain from  
99 multiple matings but, at low density, females are selected to begin searching because any  
100 delay in becoming fertilized is costly for a female (see also Kokko and Mappes 2005).

101 More generally, high search effort by females is not always linked to situations when costs are  
102 low. Evidence suggest that females are capable of expending considerable effort on mate  
103 searching even when confronted with high search costs. This is seen, for example, in the  
104 cardinal fish *Apogon niger*, where increased mobility by mate-searching females late in the  
105 breeding season is correlated positively with their rate of disappearance attributed, apparently,  
106 to mortality by predatory flounder and lizardfish (Okuda 1999). During their short life time,  
107 female butterflies *Coenonympha pamphilus* incur significant time costs by traveling to visit  
108 males at the lek (Wickman and Jansson 1997). In that species, it has been suggested that the  
109 fitness costs suffered by females, in the form of reduced fecundity, is ameliorated by potential  
110 indirect benefits of mating with males at the lek (Wickman and Jansson 1997). A similar  
111 argument has been made for pronghorn *Antilocapra americana*, an ungulate in which females  
112 in estrus spend considerable amounts of energy moving between harems before mating (Byers  
113 et al. 2005). Finally, there are also cases where both sexes invest in mate-finding traits. In  
114 many arthropods, for example, females produce pheromones, and males follow these

115 chemical trails (Greenfield 1981; Cardé and Baker 1984; Cardé and Hagaman 1984; Takács  
116 et al. 2002; Melville et al. 2003; Nahrung and Allen 2004).

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

#### 131 SELF-CONSISTENCY AND THE DEFINITION OF MATE SEARCHING

132 We develop two self-consistent models where males and females attempt to locate each other  
133 for the purpose of mating. Self-consistency means that fitness must be evaluated by taking  
134 into account the fact that total reproduction by males should equal total reproduction by  
135 females, since every individual has one mother and one father. This simple fact, termed the  
136 Fisher condition by Houston and McNamara (2005), has been shown to be surprisingly  
137 important for developing correct predictions in conceptual models of reproductive behaviors

138 (e.g., Queller 1997; Webb et al. 1999; Houston and McNamara 2002, 2005; Kokko and  
139 Jennions 2003; Arnqvist 2004; Houston et al. 2005).

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

148 Our cost-based definition of investment in mate searching resembles the definition of parental  
149 investment, namely, care that is performed at a cost to future offspring production (Trivers  
150 1972). To avoid drawing erroneous conclusions from our model, it is important to focus on  
151 these costs, because they help to distinguish between behaviors that are selected for other  
152 reasons but happen also to improve mate encounter rates, and behaviors that are selected  
153 *because* they improve mate encounter rates. For example, consider a butterfly where females  
154 have to locate resources required for the larvae to develop (e.g. a suitable host plant for  
155 oviposition). Females are obviously selected to fly until they find such a resource. For a male,  
156 it may be optimal to wait at a resource patch if he has found one, or to intercept a female that  
157 is making her way to the resource. The observation preceding a mate encounter is that a  
158 female flies towards a male; however, this should not, *sensu stricto*, be classified as  
159 investment in mate searching by the female, because no extra cost is incurred on top of what  
160 she would have expended in any case in her quest to find a suitable egg-laying patch (see also  
161 Groddeck et al. 2004). Thus  $x = 0$  in such a case. If, on the other hand, she traveled to a male

162 lek before flying to the resource patch, the extra travel time involved presumably carries  
163 some direct cost on survival and/or fecundity. Consequently, one should classify the female's  
164 behavior as investment in mate-searching,  $x > 0$ .

#### 165 SELF-CONSISTENT MODEL WITH NO SPERM COMPETITION

166 We base our models on the concept of reproductive value and invasion fitness: a strategy of  
167 mate-searching can invade if, and only if, it yields higher fitness than the resident strategy  
168 (Metz et al. 1992). Fitness in this setting is a weighted sum of the number of different types of  
169 individuals that the focal individual contributes to the population, weighted by the  
170 reproductive value of each individual type (e.g., McNamara and Houston 1986, 1996; Taylor  
171 1990). Our model is based on a continuous-time setting, for the reason that males and females  
172 may spend quite dissimilar times in parenting activities. This implies that an individual may  
173 contribute, at any given time, to the future population in three ways: by actual offspring  
174 production, by surviving itself without changing state, or by surviving and changing state. All  
175 these options are taken into account in the concept of reproductive value, following the  
176 method outlined in Härdling et al. (2003).

177 Following a tradition in the literature of sex role evolution (Clutton-Brock and Parker 1992;  
178 Parker and Simmons 1996; Wiklund et al. 1998; Kokko and Monaghan 2001; Kokko and Ots  
179 2006), we define the relevant states as 'time in' and 'time out' for both sexes (Figure 1). In  
180 our first model, mating occurs every time a male and a female meet in 'time in'. There is only  
181 one mating preceding the production of offspring, and we assume that females cannot store  
182 sperm. We thus exclude sperm competition and multiple mating within one reproductive cycle  
183 of a female. Following mating,  $g$  offspring of each sex are produced. Both parents then enter a  
184 'time out' stage (*sensu* Clutton-Brock and Parker 1992), which makes them unable to mate  
185 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  $\beta$  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;

210 Kokko and Mappes 2005). Importantly, the operational sex ratio  $\beta$  depends on searching  
 211 effort,  $\beta = \beta(x,y)$ , since searching influences mating rates and consequently also sex-specific  
 212 mortalities and the amount of time individuals spend in the ‘time in’ state. Equation (3) in  
 213 Kokko and Monaghan (2001) gives the value of  $\beta$  once mating rates are known.

214 To keep in line with our definition of mate-searching as an investment that carries costs, we  
 215 introduce a mortality cost during ‘time in’ (other types of cost could be equally easily added  
 216 to the model, such as mortality during ‘time out’, lengthening the duration of ‘time out’, or  
 217 reducing fecundity for females). Thus, for females, the mortality during ‘time in’ is  $\mu_F(x)$ ,  
 218 which is an increasing function of  $x$ , while during ‘time out’ the mortality is fixed,  $\mu_{FO}$ . For  
 219 males, the corresponding values are  $\mu_M(y)$  and  $\mu_{MO}$ . Note that in a continuous-time  
 220 formulation, the mortalities can take any value  $\mu > 0$ : values exceeding unity simply mean an  
 221 expected lifespan below 1.

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

$$225 \quad \quad \quad \mathbf{dv}/dt = \mathbf{vQ} \quad (1)$$

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

$$229 \quad \mathbf{Q} = (q_{ij}) = \begin{pmatrix} -\frac{1}{T_F} - \mu_{FO} & m_F & 0 & 0 \\ \frac{1}{T_F} & m_F(g-1) - \mu_F & 0 & m_M g \\ 0 & 0 & -\frac{1}{T_M} - \mu_{MO} & m_M \\ 0 & m_F g & \frac{1}{T_M} & m_M(g-1) - \mu_M \end{pmatrix} \quad (2)$$

230 where, for brevity, we use notation  $m_F$  for  $m_F(x,y)$ ,  $\mu_F$  for  $\mu_F(x)$ , 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  $\mathbf{v}$  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  $1/T_F$ , 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  $1/T_F$  appears as an addition in the 2nd column (the 2nd element gives  $v_{FI}$  in  $\mathbf{v}$ ) but as a  
 237 subtraction in the 1st row (corresponding to  $v_{FO}$  in  $\mathbf{v}$ ). The female may also die, which  
 238 happens at a rate  $\mu_{FO}$ , and leads to a loss of reproductive value  $v_{FO}$  and no gain — i.e. the rate  
 239  $\mu_{FO}$  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  $d\mathbf{v}^*/dt = 0$  (Härdling et al. 2003).

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

$$250 \quad v_{\text{FI}}^*/v_{\text{FO}}^* = 1 + \mu_{\text{FO}} T_{\text{F}} \quad (3a)$$

$$251 \quad v_{\text{MI}}^*/v_{\text{MO}}^* = 1 + \mu_{\text{MO}} T_{\text{M}} \quad (3b)$$

$$252 \quad \text{and} \quad v_{\text{MI}}^*/v_{\text{FI}}^* = \frac{\mu_{\text{F}}}{m_{\text{F}}} - \frac{g-1}{g} - \frac{1}{g(1+\mu_{\text{FO}})} \quad (3c)$$

253 Consider a mutant female with strategy  $x$  in a population in which  $x^*$  and  $y^*$  are in use.

254 Assume that the mutant is rare, which means that its search effort  $x$  changes its mating rate

255  $m_{\text{F}}(x)$  via its effect on  $f(x, y^*)$ , but the operational sex ratio  $\beta$  experienced by the mutant is not

256 significantly altered by its presence but determined by population-wide behavior  $x^*$  and  $y^*$ ,

257 thus  $\beta = \beta(x^*, y^*)$ . (Obviously the population may shift to a new  $x^*$  and  $y^*$  as the eventual

258 consequence of successful mutant invasion, and  $\beta$  will thus be recalculated for each pair  $\{x^*$ ,

259  $y^*\}$  when determining evolutionary trajectories). The strength of selection at  $\{x^*, y^*\}$  is a

260 partial derivative of the mutant's reproductive value  $\partial v_{\text{FI}}(x, x^*)/\partial x|_{x=x^*, y=y^*}$ , where

$$261 \quad v_{\text{FI}}(x, x^*) = e^{-r^*} [v_{\text{FO}}^* q_{11} + v_{\text{FI}}^* q_{21} + v_{\text{MI}}^* q_{41}]$$

$$262 \quad = e^{-r^*} [v_{\text{FO}}^* m_{\text{F}}(x) + v_{\text{FI}}^* [m_{\text{F}}(x)(g-1) - \mu_{\text{F}}(x)] + v_{\text{MI}}^* m_{\text{F}}(x) g] \quad (4)$$

263 Here,  $r^*$  is the continuous-time growth rate of the resident population, which equals  $r^* = 0$

264 for a population at equilibrium. Note that equation (4) is a continuous-time version of mutant

265 reproductive values such as, for example, eq. 17 in Pen et al. (1999). Using equations (3a-c)

266 and (4), we find that the selection differential for female searching equals, up to a constant of

267 proportionality,

268 
$$S_F = g \frac{1}{m_F} \frac{\partial m_F}{\partial x} - \frac{1}{\mu_F} \frac{d\mu_F}{dx} \quad (5a)$$

269 A similar derivation gives the male selection differential

270 
$$S_M = g \frac{1}{m_M} \frac{\partial m_M}{\partial y} - \frac{1}{\mu_M} \frac{d\mu_M}{dy} \quad (5b)$$

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

274 *No sperm competition: results*

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

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

288 Nevertheless, equations (5a-b) allow for the possibility that one sex performs the majority,  
289 or all, of the mate-searching. As a whole, individuals of a given sex are selected to search  
290 more if their mortality is high ( $1/\mu$  is low), if the increase in mortality by doing more  
291 searching is relatively low ( $d\mu/dt$ ), if mate-finding is currently a slow process ( $1/m$  is high),  
292 and if a significant increase in mate encounter rates can be achieved by increasing investment  
293 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  
294 by the other sex. If, for example, the outcome of searching is given by  $f(x,y) = x+y$ , then  $1/m_M$   
295  $\partial m_M/\partial y$  will be proportional to  $1/(x+y)$ . The more females search, the smaller is the incentive  
296 for males to do so ( $1/(x+y)$  decreases with increasing  $x$ ), and vice versa.

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

307 The importance of the shape of the cost function is shown by a comparison between cases  
308 where the mortality increase with mate searching is fairly linear (Figure 2a), accelerating  
309 (quadratic; Figure 2b) or strongly accelerating (Figure 2c). In the first case, we predict that  
310 only one sex searches, and initial, incidental factors determine which one it is (Figure 2a). In  
311 the second case, there is a line of neutrally stable equilibria, and populations approach any

312 point along this line, again depending on starting conditions of ancient populations. Here,  
313 both sexes may search, but they will do so to a different degree: female mate searching is  
314 inversely proportional to male mate searching. In the third case, both sexes converge towards  
315 a single equilibrium, where they invest equal effort into mate searching (Figure 2c).

316 Intuitively, one would imagine that widely differing parental roles (very different  $T_F$  and  $T_M$ )  
317 should give an *a priori* reason for males to search more than females. In our fully self-  
318 consistent life-history model, we have used a modeling approach that has become one of the  
319 standard ways to predict sex role asymmetries (Clutton-Brock and Parker 1992; Parker and  
320 Simmons 1996; Kokko and Monaghan 2001). Yet we simply reproduced one central feature  
321 of the influential model by Hammerstein and Parker (1987): the images in Figure 2 are  
322 symmetrical with respect to the diagonal, thus there is a fundamental symmetry between the  
323 sexes and either sex can end up as the searcher.

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

### 330 INTRODUCING SPERM COMPETITION

331 A close inspection of the ‘time in’–‘time out’ modeling framework, above, reveals a  
332 potentially unrealistic feature: females always commence reproduction as soon as they have  
333 mated once. Although this may be true for some taxa (speckled wood butterflies *Pararge*  
334 *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 ( $\beta$  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.



359 Since mate encounters are an intrinsically random process, there is a chance that the female  
 360 spends the mating window without meeting anyone (Kuussaari et al. 1998; Rhainds et al.  
 361 1999; Kokko and Mappes 2005), and in that case we assume that she cannot reproduce before  
 362 she has completed another mating window. Denoting by  $p$  the probability that at least one  
 363 mate has been found during a mating window, and taking note that each window is unity in  
 364 length, her rate of commencing reproduction from the ‘time in’ state now equals  $p$ . If males  
 365 are found as a Poisson process with a mean value of  $m_F(x,y)$  (which implies  $N = m_F(x,y)$ ), a  
 366 female will be unsuccessful in locating a male with probability  $e^{-m_F(x,y)}$ . Therefore,  $p =$   
 367  $1 - e^{-m_F(x,y)}$ .

368 The selection differential for females (equation 5a), up to a proportionality constant, now  
 369 takes the form

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

372 For males, the situation is different. They will suffer from reduced mating success in each  
 373 mating when females mate multiply, which correctly takes self-consistency into account, but  
 374 the gains still remain linear: every additional mating improves reproductive success equally  
 375 much. From each mating with a female, males gain  $g$  offspring if the female mates with no  
 376 other males during the mating window,  $g/2$  offspring if she mates once with someone else,  $g/3$   
 377 if twice, and so on. The expected gain from each mating is obtained from the Poisson  
 378 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 
$$S_M = b_M \frac{\partial m_M}{\partial y} - \frac{1}{\mu_M} \frac{\partial \mu_M}{\partial y}, \text{ where } b_M = g \frac{1-e^{-N}}{m_M N} \quad (7b)$$

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  $b_M/b_F$ , 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;

423 Cardé and Baker 1984; Svensson 1996; but see Blows 2002). Males, on the other hand,  
424 usually develop extreme mechanisms to follow these trails (e.g. extreme sensitivity to  
425 pheromone compounds, Angioy et al. 2003), and may often suffer considerable mortality  
426 risks following the pheromone signal (Acharya 1995; Svensson 1996).

427 Figure 6a shows evolutionary trajectories when the searching outcome is multiplicative,  $f(x,y)$   
428  $= xy$ , which necessitates some effort by both sexes before  $f(x,y) > 0$  is reached. Unsurprisingly,  
429 both sexes now spend some effort in mate location, but the overall shape of the solutions stays  
430 similar to that of figure 5: solutions become fairly symmetrical only once  $M$  is so small that  
431 multiple mating becomes fairly rare. When multiple mating is common, males perform the  
432 majority of mate-locating tasks. Figure 6b shows the effect of searching on individual  
433 mortalities. The effort that females accept to spend will have minute costs: they evolve to  
434 accept a mortality increase of less than 0.01%, when they find, on average, 10 or more mates  
435 (two leftmost dots in Figure 6b). Males, in the meanwhile, accept much higher costs.  
436 However, if an average female finds less than 4 males during a mating window, mortality  
437 increases of more than 10% become acceptable for both sexes, and in extreme cases ( $N = 1.28$   
438 in the rightmost dot, Figure 6b, indicates an  $\exp(-1.28) = 27.8\%$  risk of remaining unmated)  
439 both females and males can perform activities that double their mortality, if these improve  
440 mate encounter rates sufficiently.

#### 441 DISCUSSION

442 Recent theoretical literature has highlighted the need to reanalyze conflicts where  
443 reproductive activities can, in principle, be performed by either sex but, in reality, show  
444 strong sex biases. For example, female-biased parental care does not immediately follow from  
445 the fact that males can potentially reproduce more often than females. This is because actual  
446 (rather than potential) mating rates must be equal across the two sexes (e.g., Queller 1997;

447 Kokko and Jennions 2003; Arnqvist 2004; Kokko et al. 2006), and models must take this  
448 into account to be self-consistent (Houston et al. 2005; Houston and McNamara 2005). This  
449 so-called Fisher condition (*sensu* Houston and McNamara 2005) has important consequences  
450 for mate searching. The intuitive reasoning, that males search because a high potential  
451 reproductive rate imposes high opportunity costs on them if they do not search, turns out to be  
452 fragile (Hammerstein and Parker 1987). If we assume that the production of offspring  
453 immediately follows every mating (i.e. no sperm competition), either sex can end up  
454 assuming the searching role, and males should be no more likely to take on the greater search  
455 effort than females even if the sexes differ in parental investment. The reason why the  
456 opportunity cost argument fails is that a male cannot mate if there are no females available to  
457 mate with, and the Fisher condition guarantees that males on average do not reproduce any  
458 faster than females. Instead, our results predict either divergence (the sex that ancestrally  
459 searched more ends up taking the searching role, i.e. the “two ESS” solution found by  
460 Hammerstein and Parker 1987) or convergence, where both sexes search equally much. In  
461 either case, any notion that males should be automatically directed to the searching role  
462 merely because of differences in gametic investment remains unsupported.

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

469 *Does the ubiquity of male searching reflect the ubiquity of sex-specific costs?*

470 Sex differences in costs are probably common because males and females typically differ  
471 from each other in many aspects of their reproductive biology, and any differences such as  
472 size dimorphism or elaborate ornaments could cause the direct costs of searching (such as  
473 mortality) to differ between the sexes. Nevertheless, we consider it unlikely that sex-specific  
474 costs can explain the ubiquity of male searching in nature. For this hypothesis to generally  
475 favor male mate searching, costs should be systematically higher for females. It has been  
476 argued that this is the case when females already suffer high costs associated with some other  
477 aspect of reproduction. Greenfield (1981), for instance, suggested that mate-searching by  
478 female moths would represent a considerable cost in addition to those already incurred from  
479 having to locate larval food resources for oviposition. Nevertheless, modeling shows that this  
480 intuitive argument can be surprisingly fragile.

481 The argument for why this should be the case requires considering both immediate and  
482 delayed costs of mate-searching effort, and we will first consider immediate costs. Our model  
483 assumes that mate-searching increases mortality in either females or males for the duration of  
484 time that they search (i.e. once they mate, this immediate threat is removed). The model  
485 predicts an asymmetry in the search effort if this immediate increase in mortality is larger for  
486 one of the sexes, but this prediction is independent of any other life history difference. If there  
487 is, for example, sexual size dimorphism, this may select for searching by the smaller sex if  
488 small individuals are better able to avoid predation while moving. But if predation is size-  
489 independent, then no sex difference is predicted despite the fact that the large and the small  
490 sex otherwise may follow different life histories (e.g. their vulnerability to starvation may  
491 differ). Thus, to evaluate if immediate costs support the role of the sex-specific hypothesis as  
492 an explanation of male mate searching, one needs to estimate if mortality per unit of searching  
493 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 in 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



542 where variation in population density (or some other environmental factor that influences  
543 mate encounter rates) covaries with mate searching costs, while leaving mate encounter rates  
544 relatively unchanged (meaning that female mating chances do not vary significantly with  
545 mate encounter rates). The easiest imaginable situation is a case where densities vary but are  
546 always quite high, as in the fiddler crab example discussed above. Here, mate finding per se is  
547 not difficult for females, but sampling several males can be more costly than finding just one,  
548 and this cost may decrease with increasing density (see also deRivera 2005).

549 *The ubiquity of male searching most likely reflects the ubiquity of multiple mating*

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

563 The multiple mating hypothesis predicts a shift towards greater mate searching effort by  
564 females when mate availability is low. Under these conditions females do not mate with very  
565 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

590 conditions according to the multiple mating hypothesis, but in high density according to the  
591 sex-specific cost hypothesis.

592 *Further possibilities*

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

609 Our model was designed to investigate the most basic form of mate searching, where potential  
610 mates do not differ in any direct or indirect benefits provided (nor is multiple mating assumed  
611 to be detrimental to either sex, but see Arnqvist and Rowe 2005). While this assumption is a  
612 necessary first step in a general model of the evolution of mate-location traits, an obvious next  
613 step is to incorporate the possibility of mate sampling to improve mate quality (Byers et al.

614 2005; Dunn and Whittingham 2007), perhaps together with costs or benefits of multiple  
615 mating. This could potentially increase the prevalence of female searching if mate-search  
616 improves mate quality, and provide an additional reason why sex-specific searching patterns  
617 can respond to density. For example, the prospects of finding a high quality male may become  
618 worthwhile at high density where there are many males to choose from, while at low density  
619 such prospects might be too poor to pursue (Kokko and Rankin 2006). This could potentially  
620 help to explain why the mate searching behaviors of, for example, the butterfly *Coenonympha*  
621 *pamphilus* (Wickman and Jansson 1997) and the California fiddler crab *Uca crenulata*  
622 (deRivera 2005) appear to fit the sex-specific cost hypothesis better than the multiple mating  
623 hypothesis. In the most complicated scenarios, females gain by choosing mates but also pay  
624 costs of mate sampling, both can vary with density, but changing female behavior with  
625 density implies that the prevalence of multiple mating varies too. Therefore, while the sex-  
626 specific cost and the multiple mating hypothesis do not perform equally well when attempting  
627 to explain general patterns, they may have to be considered together (rather than as mutually  
628 exclusive alternatives) when considering specific cases.

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## FIGURE LEGENDS

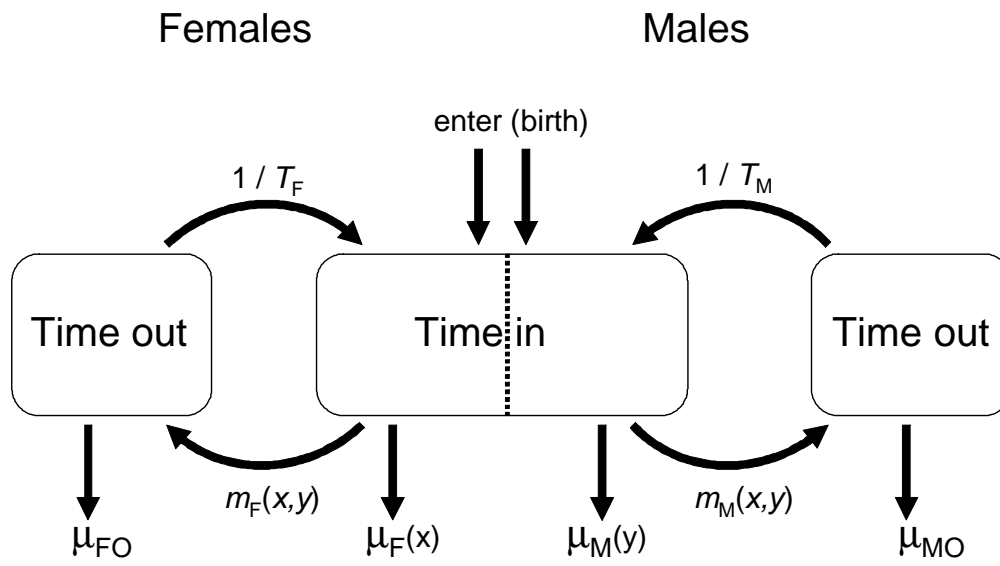
- 795
- 796 Fig. 1 Flow diagram of the model. Females and males encounter each other when they  
 797 are in ‘time in’; after mating, both sexes enter a ‘time out’ stage, but the length of  
 798 this can be different for the two sexes. Mating rates can differ between the sexes  
 799 too, because of a different number of males and females in the ‘time in’ stage.
- 800 Fig. 2 Evolutionary trajectories without sperm competition, when evolutionary change  
 801 per generation is proportional to the LHS of eqs. 5a for females, and 5b for males.  
 802 The dashed diagonal indicates equal searching by males and females. In (a),  
 803 selection always favors increased searching effort in the sex that initially searches  
 804 more. In (b), there is a continuum of neutral equilibria indicated with the heavy  
 805 solid line, and examples of single equilibria are indicated with dots. Parameters:  
 806  $T_F = 1$ ,  $T_M = 0.01$ ,  $M = 1$  (though these parameters do not influence solutions as  
 807 long as there is no sperm competition, see eqs. 5a-b),  $g = 2$ ,  $f(x,y) = x+y$ ,  $\mu_{FO} =$   
 808  $\mu_{MO} = 0.1$ , and (a)  $\mu_F(x) = 0.1 (1+x^{1.2})$  and  $\mu_M(y) = 0.1 (1+y^{1.2})$ , (b)  $\mu_F(x) = 0.1$   
 809  $(1+x^2)$  and  $\mu_M(y) = 0.1 (1+y^2)$ , (c)  $\mu_F(x) = 0.1 (1+x^{2.5})$  and  $\mu_M(y) = 0.1 (1+y^{2.5})$ .
- 810 Fig. 3 Evolutionary trajectories without sperm competition can become asymmetrical if  
 811 costs of searching differ between the sexes. Solutions and parameter values are  
 812 calculated as in figure 2b, but now with a non-linear searching outcome  $f(x,y) =$   
 813  $\sqrt{x+y}$ , and (a) equal costs for each sex,  $\mu_F(x) = 0.1 (1+x^{1.2})$  and  $\mu_M(y) = 0.1$   
 814  $(1+y^{1.2})$ , or (b) female search cost is 50% higher,  $\mu_F(x) = 0.1 (1+1.5x^{1.2})$  and  $\mu_M(y)$   
 815  $= 0.1 (1+y^{1.2})$ .
- 816 Fig. 4 The Bateman gradients, i.e. the reproductive benefits  $b_M$  and  $b_F$  for female and  
 817 males, respectively, from improved mate encounter rates, and the ratio  $b_M/b_F$ , for

818 different values of the average number of matings per mating window,  $N$ . The  
 819 decrease in both  $b_F$  and  $b_M$  with  $N$  reflects that each mating becomes less  
 820 important as a determinant of fitness. However, the decrease in  $b_F$  is much  
 821 steeper, therefore  $b_M/b_F > 1$  which implies stronger selection for males to search  
 822 for mates. Figure is calculated with  $g = 1$  and  $m_M = 1$ . A lower value of  $m_M$  (e.g.  
 823 due to a male-biased OSR) would further exaggerate the difference between  $b_M$   
 824 and  $b_F$ , while  $g$  has no effect on  $b_M/b_F$ .

825 Fig. 5 Evolutionary trajectories with sperm competition. Solutions and parameter values  
 826 as in figure 2b, but now the different curves do not correspond to different starting  
 827 points  $\{x,y\}$  but to different values of species-specific mate encounter rate,  $M$ .  $M$   
 828 takes values, from left to right,  $M = 100, 50, 20, 10, 5, 3, 2, 1, 0.5$ , and  $0.1$ . In (a),  
 829 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),  
 830 costs are more linear than in (a):  $\mu_F(x) = 0.1 (1+x^{1.8})$  and  $\mu_M(y) = 0.1 (1+y^{1.8})$ .  
 831 Except for extremely low mate encounter rates in (b), there is a single equilibrium  
 832 in each case, and males search more than females. At the equilibrium marked with  
 833 a dot, the value of  $N$  becomes (from left to right) (a) 432, 170, 50, 19.9, 7.9, 4.4,  
 834 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  
 835 the female-searching equilibrium) 0.37. Note that females search almost as much  
 836 as males when low  $M$  limits multiple mating (equilibria with low  $N$ ).

837 Fig. 6 Evolutionary trajectories with sperm competition, when some activity is required  
 838 from both sexes before mates can find each other:  $f(x,y) = xy$ . Other values as in  
 839 Figure 5a, except that  $M$  takes values (from left to right)  $M = 100, 50, 20, 10, 5, 3,$   
 840  $2, 1$ , leading to  $N = 13.1, 10.8, 7.6, 5.4, 3.6, 2.53, 1.93$  and  $1.28$ . In (a), the raw  
 841 values of  $x$  and  $y$  are given, while in (b) investment in mate-searching is graphed

842 as the proportional increase in mortality during 'time in' caused by mate  
843 searching,  $\mu_F(x)/\mu_F(0)$  and  $\mu_M(y)/\mu_M(0)$ . When mate encounter rates are high to  
844 moderate, females pay extremely low costs for their searching (the 'pheromone'  
845 case), while lowest mate encounter rates may make both sexes increase their  
846 mortality by 100% or more (i.e. more than halve their survival).



847

848 Fig. 1.

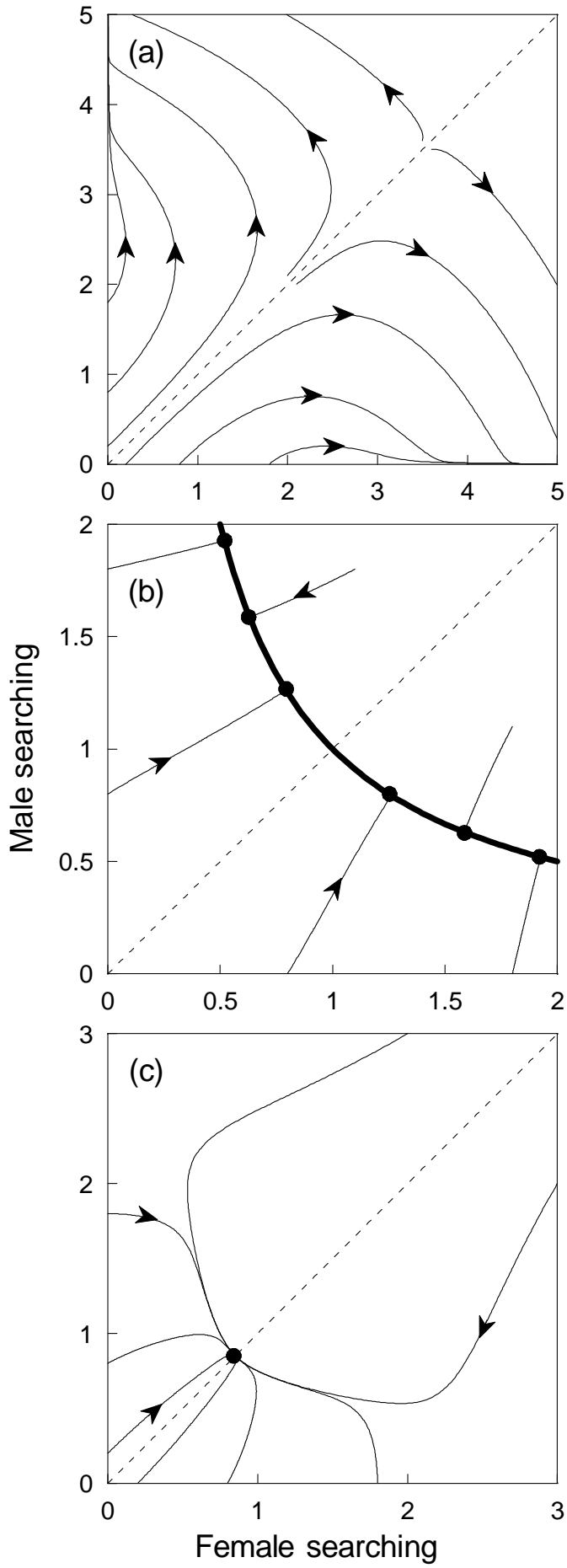
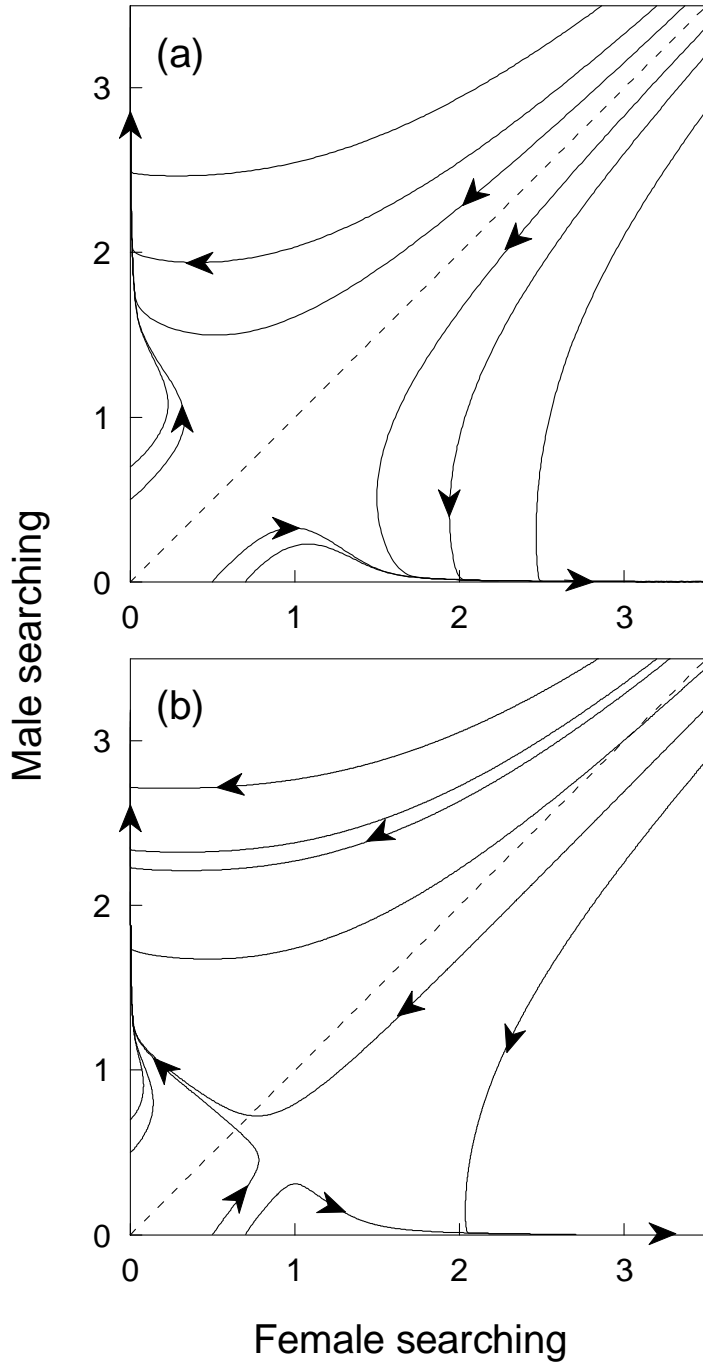


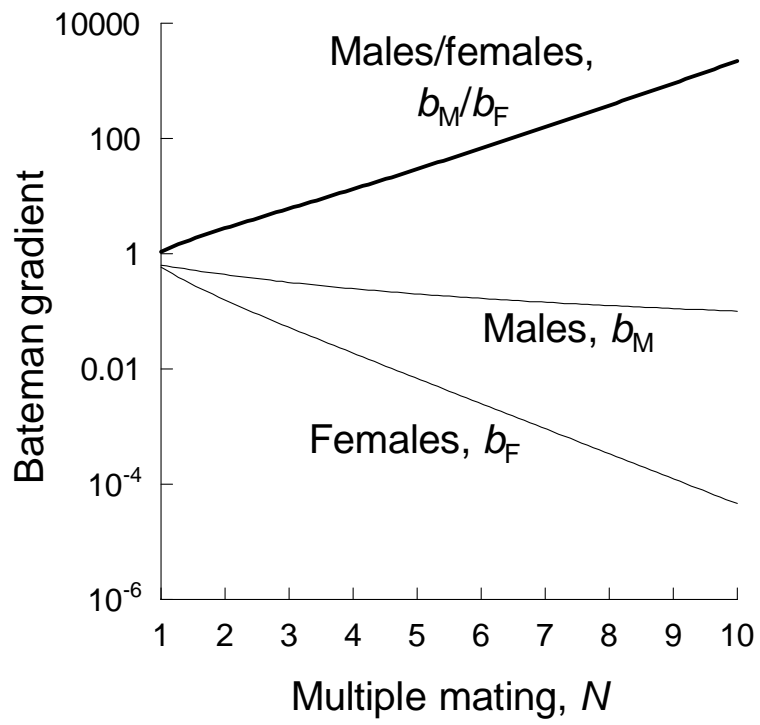
Fig. 2



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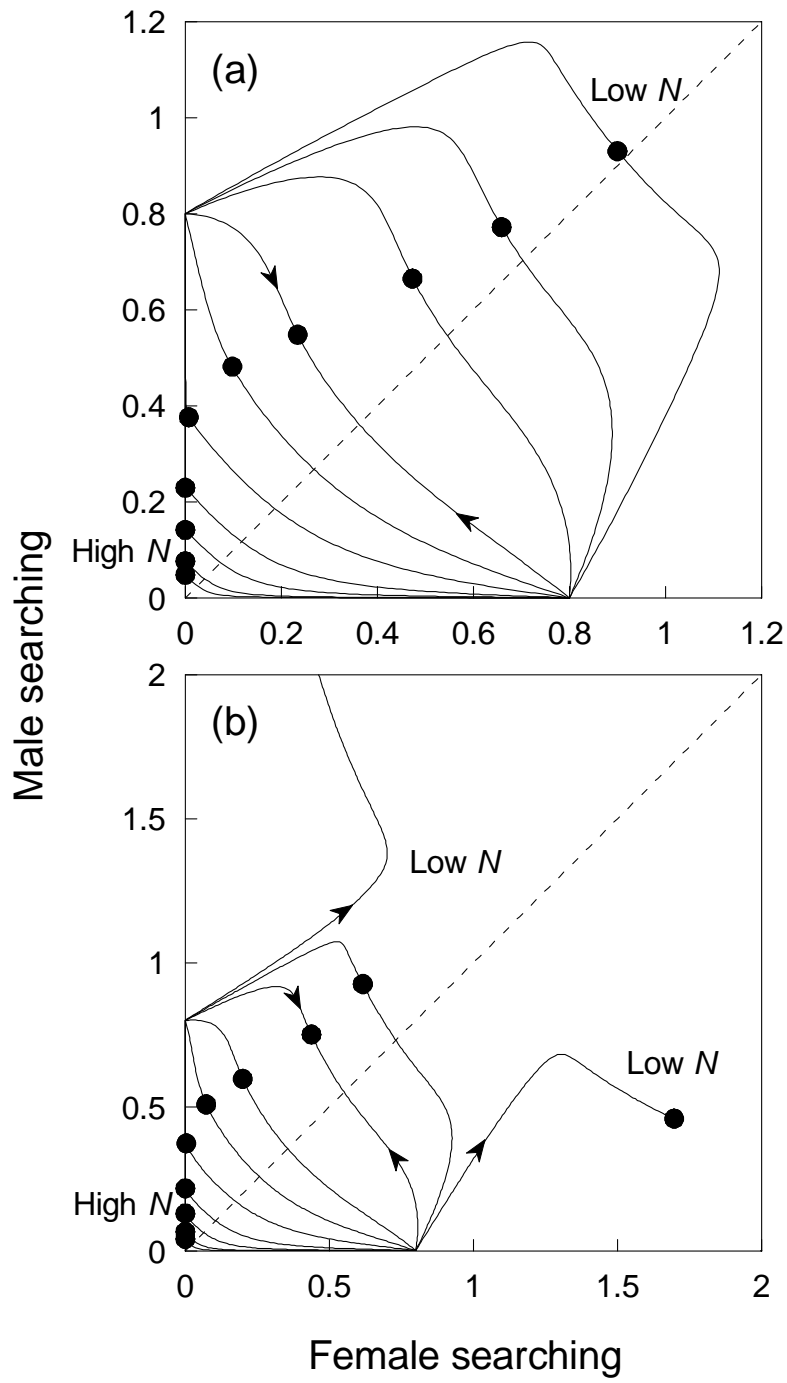
Fig. 3

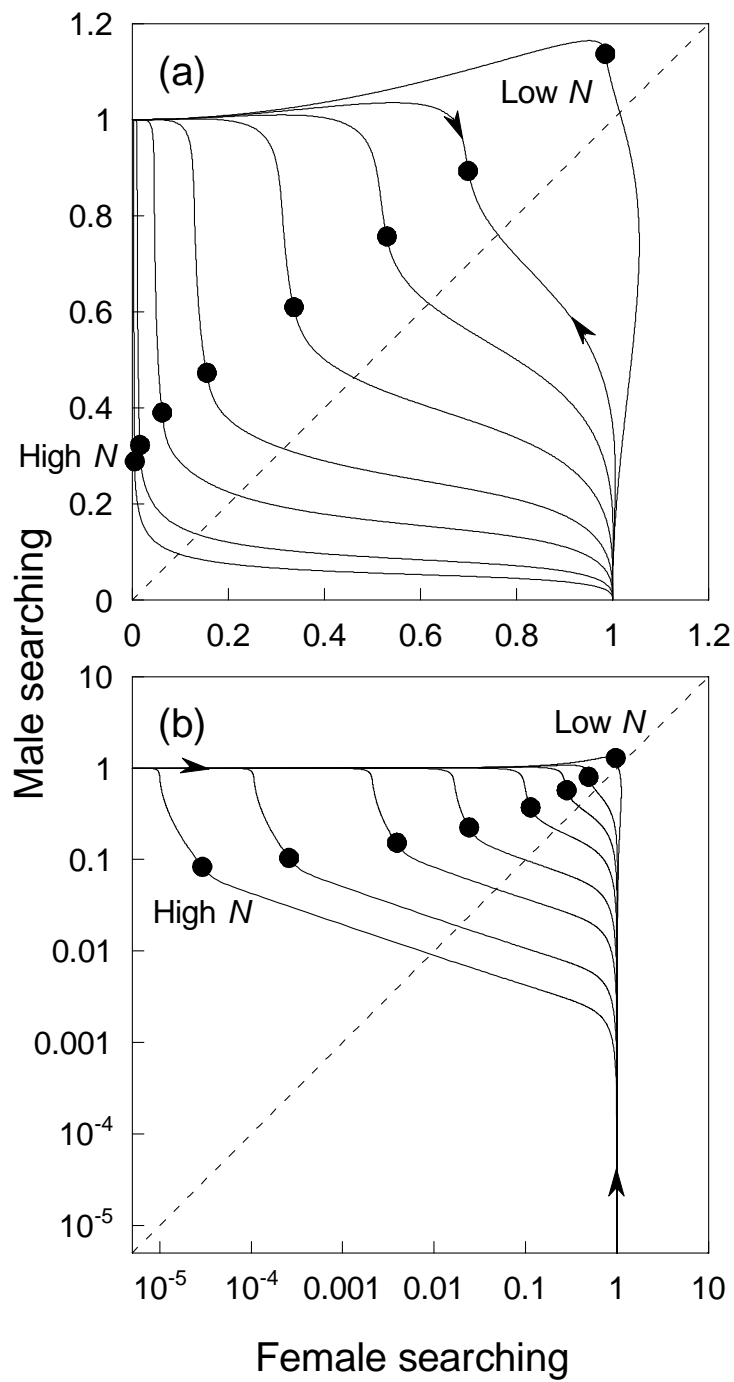




851

852 Fig. 4





854

Fig. 6

855