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## Resolving Conflict Over Within-Pair Mating Rate in External Fertilizers

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Running Head: Repeated Mating in External Fertilizers

19

20

## Abstract

21 Besides egg fertilization, females of many taxa obtain direct fitness benefits from male mates,  
22 such as food, protection or paternal care. But males often increase their own fitness by mating  
23 with several females, among which they distribute sperm along with the above-mentioned  
24 benefits, reducing the benefits to individual females. These diverging interests lead to a conflict  
25 in which each female may try to ensure male fidelity and get exclusive access to male-provided  
26 benefits. Here, we use a theoretical model to show how a female of an externally fertilizing  
27 species may achieve mate fidelity by soliciting copulations at such a rate that the male has  
28 insufficient sperm left to increase his fitness with additional females. We show that three  
29 alternative condition-dependent evolutionarily stable mating relationships emerge in this  
30 scenario, based on whether one mate's preference for mating rate dominates, or the conflict is  
31 resolved by what amounts to negotiation. We demonstrate how these outcomes depend on some  
32 features of physiology, ecology, and behavior. In particular, a greater reproductive benefit to a  
33 female from exclusive access to a male partner—or the occasional tendency of females to  
34 withhold eggs during mating—can increase male fidelity; and continuous sperm regeneration  
35 rather than an initially-set stock of sperm allows for multiple within-pair mating across all three  
36 mating patterns.

37

38 Key Words: Game theory, male care, monogamy, sexual conflict, sperm supply.

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53 preparation (PHC); writing and editing (PHC, CT); final approval (PHC, CT)

54

55

## Introduction

56 Females often mate with multiple males to gain additional resources (Arnqvist and  
57 Nilsson, 2000; Hosken and Stockley, 2003) or to obtain good genes for offspring (Halliday and  
58 Arnold, 1987; Jennions and Petrie, 2000). This may even be true for some socially monogamous  
59 females (Birkhead and Moller, 1992). But why do permanently or sequentially monogamous  
60 females often mate repeatedly with the same mate, despite possible energetic or risk-related  
61 mating costs (Daly, 1978)? While multiple mating by females (polyandry) has been the focus of  
62 many theoretical models, within-pair repeated mating has received much less attention.

63 Petrie (1992) and Hunter et al. (1993) reviewed empirical work on repeated mating  
64 (mainly in birds) and proposed several hypotheses pertaining to fertilization insurance, mate  
65 choice or mate guarding. In particular Petrie (1992) suggested that a female may mate repeatedly  
66 with her partner in order to manipulate him into monogamy, thereby securing exclusive access to  
67 his gametes, his good genes or the direct benefits he provides. In the context of sexual conflict  
68 (Chapman et al., 2003), this hypothesis can be conceptualized as a negotiation game between  
69 mates for access to gametes and support, where females would trade copulation, hence  
70 opportunity for fertilization, for male-provided dilutable benefits (i.e. benefits which are shared  
71 among the male's partners; Tazzyman et al., 2012).

72 Petrie's hypothesis is both appealing and supported by some observations (Hunter et al.,  
73 1993; Petrie, 1992) but the evolutionary stability of such a strategy has not been assessed. In  
74 particular, whether repeated mating may resolve sexual conflict over mate fidelity could depend  
75 not only on the magnitude of male-provided benefits, but also on the relative capacity of both  
76 males and females to sustain a high mating rate. The patterns of gamete production and release  
77 are therefore likely to play a central role in the evolution of within-pair repeated mating. The aim

78 of the model presented here is to explore how gamete management may affect the evolutionarily  
79 stability of within-pair repeated mating as a female strategy to secure exclusive access to male  
80 provided benefits.

81         The role of gamete management in the evolution of conflict over mating rate has been  
82 addressed mainly in the context of sperm competition in polygynandrous internal fertilizers (Abe  
83 and Kamimura, 2015; Parker, 1998, 1970a; Parker and Pizzari, 2010), and to a lesser extent in  
84 the context of fertilization efficiency in external fertilizers with no sperm competition (Kiflawi,  
85 2000; Shapiro and Giraldeau, 1996). Models developed in both contexts indicate that under the  
86 risk of sperm limitation, males may maximize reproductive success by adjusting ejaculate size to  
87 the risk of sperm competition and to the number of eggs released by the female, which she sets  
88 with her own reproductive success at stake. In response to ejaculate size, high mating rate could  
89 be a way for females to ensure fertilization of their eggs by sperm of males that prudently  
90 allocate their ejaculates between partners (Alonzo and Pizzari, 2013; Kiflawi, 2000; Wedell et  
91 al., 2002).

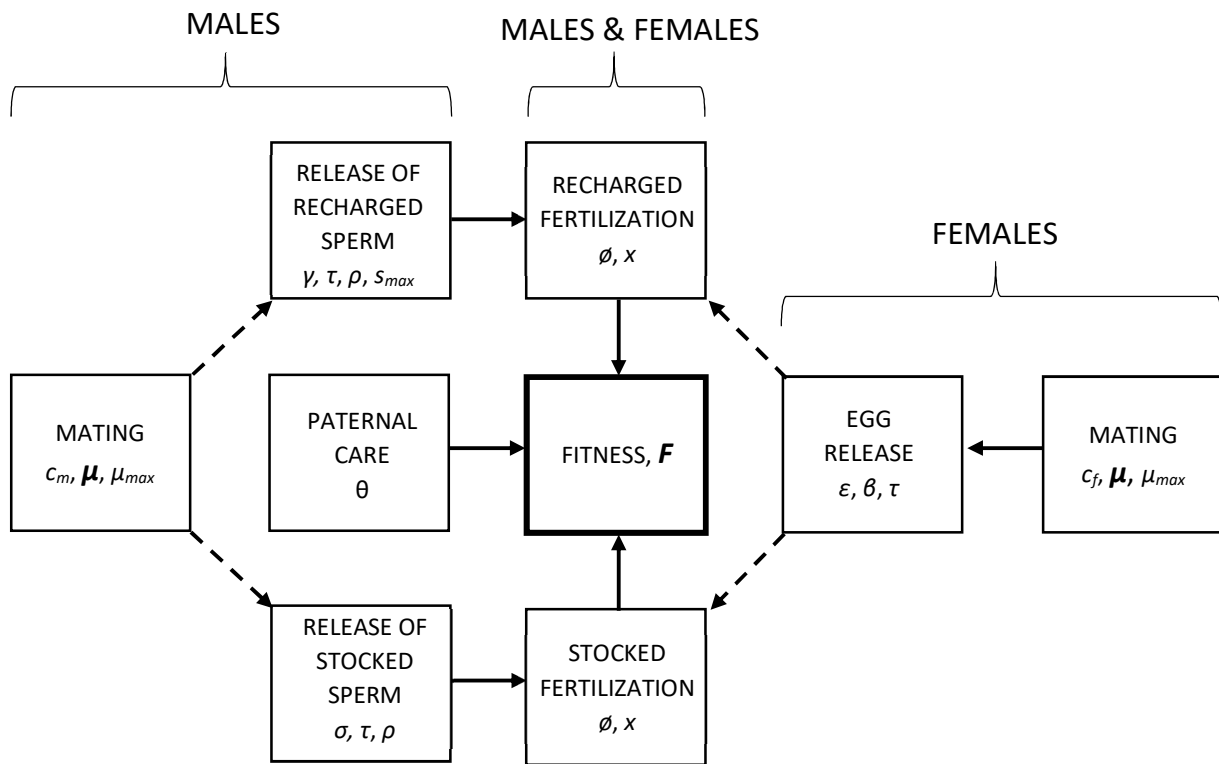
92         Sperm economics mainly accounts for the total amount of sperm available to males  
93 (assessed by testis size; Lüpold et al., 2020) and the way this stock is parceled among mating  
94 occasions. Models addressing the evolution of mating rate do not clearly account for the  
95 dynamics of sperm production, although the pattern of sperm production is likely to constrain the  
96 evolution of mating rate. In some species, males start the mating season with a finite stock of  
97 sperm that cannot be replenished (Boivin et al., 2005; Michalik and Lipke, 2013; Wootton and  
98 Smith, 2014). In other species, males can replenish their sperm stock after a refractory period  
99 that may vary among and within species (Dewsbury, 1982; O’Dea et al., 2014).

100 In this article, we set sperm competition aside and focus on external fertilizers, which pair  
101 in nests where males provide dilutable benefits to females and offspring. Many fish species  
102 correspond to these characteristics (Wootton and Smith, 2014). Although alternative  
103 reproductive tactics exist (Taborsky, 2008), the incapacity of females to store sperm limits the  
104 scope for sperm competition in external fertilizers (Fitzpatrick, 2020). On the other hand,  
105 external fertilization often allows females to control mating rate and the number of eggs released  
106 per mating. On some occasions females may even solicit mating but withhold eggs, thereby  
107 increasing mating rate (and sperm expenditure by males) but not fertilization (Jones and Ball,  
108 1954; Esteve, 2007; Schneider, 1971; Ridgway et al., 1989; Roy and Pal, 1986; Yamazaki and  
109 Koizumi, 2017; Petersson and Järvi, 2001). Moreover, males can either start the mating period  
110 with a finite stock of sperm or replenish it throughout the season (O’Dea et al., 2014), and they  
111 often provide direct benefits such as paternal care in the nest they build (Gross and Sargent,  
112 1985). Within-pair repeated mating is sometimes observed in such species (Johnson et al., 2015).

113 Our goal is therefore to predict how gamete management affects the resolution of male-  
114 female conflict over mating rate in external fertilizers with no sperm competition but with male-  
115 provided benefits (i.e. to build a “resolution” model, sensu Parker, 2006). To do this, we derive  
116 and analyze a simple game theoretic model based on finding the ESS mating rate for a single  
117 mating season and the use of all available gametes, nest building, and external fertilization  
118 (Figure 1), from which we derive the expected mating patterns. This enables us to address the  
119 following four questions:

- 120 (1) How can sexual conflict over within-pair mating rate be resolved for external fertilizers?
- 121 (2) How does this resolution depend on whether or not males continually regenerate sperm?
- 122 (3) How do the mating patterns depend on the efficacy of male help at the nest?

123 (4) Why might females sometimes withhold eggs during mating bouts?



124  
 125 **Figure 1** Overview diagram of mating and reproductive success in the model. Variables (**bold**  
 126 italics) and parameters (italics) are associated with each sex-specific process. Fitness (***F***) here is  
 127 based on expected number of offspring produced at the end of parental care. Mating rate (***μ***) is  
 128 the only variable that can evolve. Arrows indicate causal sequences; dashed arrows are  
 129 alternatives that depend on whether sperm are continuously recharged or stocked at maturation.

130

131 **Methods**

132 As a biological grounding for the derivation, we envision an externally fertilizing,  
 133 semelparous, nest building, pair bonding species, such as many fishes (Wootton and Smith,  
 134 2014). Our model is deterministic, using fixed parameter magnitudes to obtain what can be



135 considered expectations from an underlying stochastic formulation. We emphasize that a  
 136 stochastic version of the dynamics we depict may yield somewhat different results.

137 We begin by assuming that constant numbers of eggs and sperm, specifically  $E$  and  $S$ , are  
 138 released by mates in each mating bout. We assume that the ratio of sperm released to eggs  
 139 released during a mating bout determines the fertilization efficiency  $\lambda$ , but with two important  
 140 caveats. (1) A larger number of eggs released by a mating female should generally provide a  
 141 denser target for sperm to encounter them more efficiently; in other words, each individual  
 142 sperm has a chance of encountering an egg that increases per egg with greater numbers of eggs  
 143 released (Vogel et al., 1982). We represent this effect in the sperm-to-egg ratio by raising the  
 144 number of eggs  $E$  to the power  $x$ , where  $0 < x \leq 1$ . (2) Fertilization efficiency  $\lambda$  should increase  
 145 with the sperm-to-egg ratio (as modified in caveat (1)) but with diminishing returns, so that very  
 146 high ratios approach the maximum efficiency of 1 (Lehtonen and Dardare, 2019). We represent  
 147 this effect with the exponential function

$$148 \quad \lambda = 1 - e^{-\vartheta \left(\frac{S}{E^x}\right)} = 1 - e^{-\vartheta S E^{-x}}, \quad (1)$$

149 where  $\vartheta$  is the coefficient determining how rapidly the efficiency approaches its upper limit with  
 150 increasing sperm-to-egg ratio. See Table 1 for a list of all model parameters, definitions, standard  
 151 or default magnitudes, and units.

152 Table 1. Parameters of the Model

153			Default	
154	<u>Symbol</u>	<u>Definition</u>	<u>Magnitude<sup>a</sup></u>	<u>Units</u>
155	$\varepsilon$	Total number of eggs per female	50,000	eggs

156	$x$	Egg number exponent for fertilization efficiency	0.8	dimensionless
157	$\beta$	Proportion of matings with no eggs released	0	dimensionless
158	$\sigma$	Total number of sperm per male (stocked sperm)	$1.5 \times 10^7$	sperm
159	$s_{max}$	Maximum recharged sperm per mating bout	50,000	sperm
160	$\phi$	Sperm:egg saturation coefficient for fertilization	0.003	per-bout sperm <sup>-1</sup> eggs <sup>x</sup>
161	$\gamma$	Sperm production coefficient (sperm recharge)	3	matings/hour
162	$\rho$	Sperm reserve proportion (sperm recharge)	0.2	dimensionless
163	$\tau$	Total duration of the reproductive interval	96	hours
164	$\theta$	Fitness multiplier accounting for male help	1.5	dimensionless
165	$c_f$	Fitness cost coefficient for a female per mating	0.01	hours/mating
166	$c_m$	Fitness cost coefficient for a male per mating	0.005	hours/mating
167	$\mu_{max}$	Maximum possible mating rate	30	matings/hour

168 \_\_\_\_\_

169 <sup>a</sup>These parameter magnitudes are loosely based on published (Applegate 1950; Yamazaki and  
170 Koizumi 2017; Docker et al. 2019) and unpublished (CT, personal observations) data for the sea  
171 lamprey, *Petromyzon marinus* (Linnaeus, 1758).

172

173 Next we determine the number of eggs released during mating. Suppose a female at  
174 maturity contains her full complement of  $\varepsilon$  eggs that can be released for external fertilization

175 during mating events. We assume that she spends the duration  $\tau$  of her reproductive interval with  
176 a single male partner. With the help of this partner, she constructs and maintains a nest where  
177 eggs are released, fertilized, tended, and protected to benefit their survival and initial  
178 development. We assume that mating happens at some consistent frequency  $\mu$  to use up all eggs  
179 during  $\tau$ , which would imply the release of  $E = \varepsilon / (\mu\tau)$  eggs at each mating. However, we also  
180 allow for the possibility that females fail to release any eggs in the proportion  $\beta$  of matings, as  
181 documented in some fishes (Esteve, 2007; Jones and Ball, 1954; Ridgway et al., 1989; Roy and  
182 Pal, 1986; Schneider, 1971; Yamazaki and Koizumi, 2017). As a result, the number of eggs  
183 released when eggs are not withheld,  $E$ , would need to be

$$184 \quad E = \varepsilon / ((1 - \beta)\mu\tau), \quad (2)$$

185 so that all eggs are released during time  $\tau$ . To address whether egg withholding could be  
186 beneficial to the female (question 4 in the introduction), we assessed the effect of variation in  $\beta$   
187 on the mating rate at equilibrium and on fitness. However, for the sake of simplicity,  $\beta$  was not  
188 allowed to evolve in the model, and the mating rate,  $\mu$ , was the only evolving variable. We  
189 assume that mating rate has an upper limit at  $\mu_{max}$ , determined by physiological and behavioral  
190 constraints on the initiation, continuation, and termination of mating events. As often observed in  
191 externally fertilizing fishes, the female is assumed to solicit matings by adopting a specific  
192 posture, and the male is assumed both to accept these solicitations to the extent allowed by his  
193 sperm supply, and to be unable to force matings.

194 In the next two sections below, we address alternative ways that sperm release at each  
195 mating,  $S$ , is determined.

#### 196 Sperm Stocked at Maturation

197 Analogous to the stock of eggs, a maturing male may have a fixed amount of sperm  $\sigma$   
198 available to expend during the entire mating interval of duration  $\tau$  (Boivin et al., 2005; Docker et  
199 al., 2019; Michalik and Lipke, 2013; Wootton and Smith, 2014). He allocates  $S$  sperm per bout,  
200 dispensing all available sperm during  $\tau$ . For males with a single mate, we allow for withholding  
201 the fraction  $\rho$  from each sperm release to allow for opportunistic mating or for the recruiting of  
202 an additional mate (Cornwallis and Birkhead, 2006). This means that

$$203 \quad S_1 = \frac{(1-\rho)\sigma}{(\mu\tau)}. \quad (3)$$

204 Here,  $S_1$  has the subscript 1 to indicate that the male has a single mate.

205 In some cases, males could benefit from attracting and securing exclusive access to two  
206 mates simultaneously, in the same or in different nests, despite the possible reduction in sperm  
207 available to each mate (Warner et al., 1995). The male with two mates must mate twice as often  
208 as each female, with the mating interval  $1/(2\mu)$ , to prevent the females from abandoning the nest  
209 in search of the higher mating rate consistent with better overall fertilization of her egg supply,  
210 given sperm limitation. We assume available alternative mating opportunities here. In this two-  
211 female case, we assume for simplicity that the male uses his entire reserve at each mating to  
212 address the additional demand (i.e.  $\rho = 0$ ), shifting sperm accumulation and thus the number of  
213 sperm released in each mating by a male with two mates  $S_2$  to

$$214 \quad S_2 = \frac{\sigma}{(2\mu\tau)}, \quad (4)$$

215 where the subscript 2 indicates that the sperm supply is shared between the two females.

216 We emphasize the contrasting levels of sperm release in  $S_1$  and  $S_2$ , where the subdivided  
 217 sperm supply reducing sperm release per mating bout in  $S_2$  and possible sperm withholding ( $\rho >$   
 218 0) in  $S_1$  determine their relative magnitudes.

### 219 Sperm Recharge

220 Here we assume that males, rather than having a fixed stock, produce sperm continuously  
 221 over time  $t$  between matings at a rate that declines as the sperm storage limit  $s_{max}$  is approached  
 222 (O’Dea et al., 2014). This process is characterized by the exponential function  $s(t) =$   
 223  $s_{max}(1 - e^{-\gamma t})$ , where  $s(t)$  is sperm availability after accumulation over time  $t$ , and  $\gamma$  is the  
 224 sperm production coefficient (Figure 2A). Males maximize sperm production when they use all  
 225 of their available stock at each mating. This is because each cycle of sperm production and  
 226 release in this case is based on the interval of highest sperm production in Figure 2A. So, with  
 227  $1/\mu$  as the interval between mating bouts, the number of sperm released per bout  $S$  with sperm  
 228 recharge becomes  $S = s\left(\frac{1}{\mu}\right) = s_{max}\left(1 - e^{-\frac{\gamma}{\mu}}\right)$ . But in this case, as for a fixed stock of sperm,  
 229 males may benefit by maintaining a sperm reserve after each mating, despite a reduced sperm  
 230 production efficiency and sperm release per mating bout. Let the parameter  $\rho$  be the proportion  
 231 of  $s(1/\mu)$  held in reserve and not released. Then the single-mate sperm release with sperm  
 232 recharge becomes

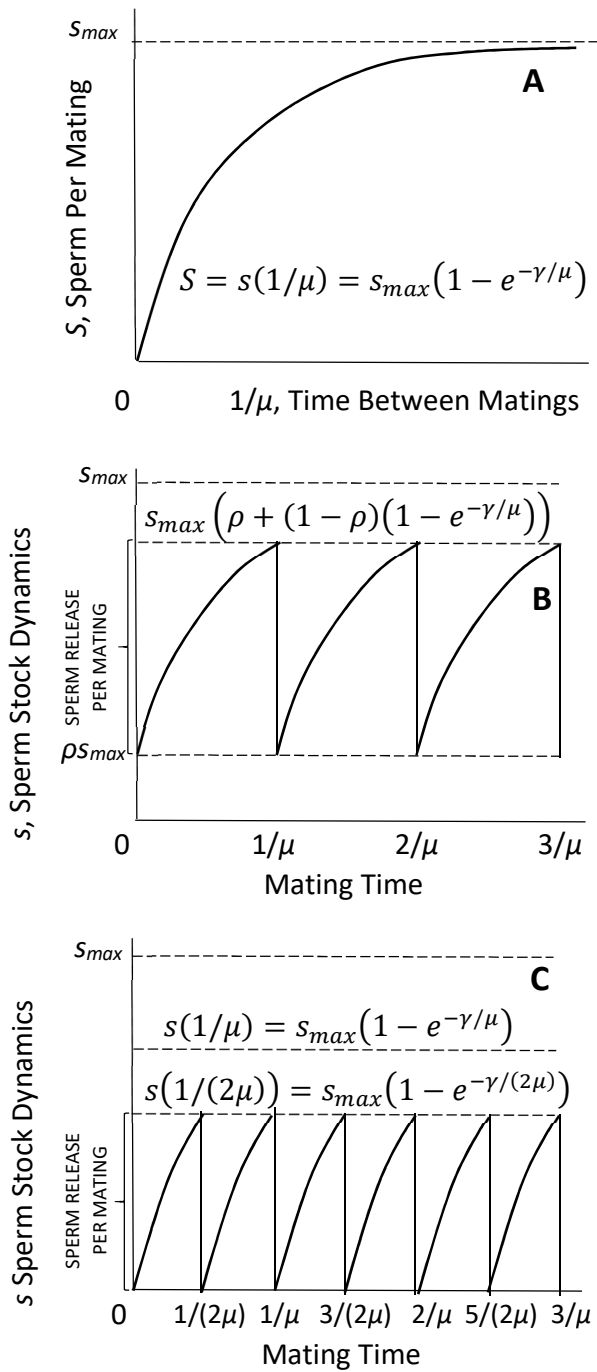
$$233 \quad S_1 = (1 - \rho)s_{max}\left(1 - e^{-\gamma/\mu}\right). \quad (5)$$

234 See Figure 2B. Following the assumptions that having two mates doubles the male’s frequency  
 235 of mating, and that the male in this case expends all available sperm in each mating bout (i.e.  $\beta =$   
 236 0), we have

237  $S_2 = s(1/(2\mu)) = s_{max} \left( 1 - e^{-\frac{\gamma}{(2\mu)}} \right).$  (6)

238 See Figure 2C.

239 To summarize this section, we have developed mathematical relationships to represent  
240 sperm release in a mating bout as a function of mating frequency when sperm are continually  
241 recharged. These relationships depend on whether a male is mating regularly with one or with  
242 two females, and whether males store some sperm between mating bouts.



243

244 Figure 2 Dynamics of continuous sperm recharge. **A.** Sperm per mating  $S = s(1/\mu)$ , where males  
 245 that mate at frequency  $\mu$  can produce sperm between mating bouts over time the time  $1/\mu$ . Sperm  
 246 are produced with diminishing returns as the stock approaches the storage limit  $s_{max}$ . The

247 coefficient  $\gamma$  is the rate constant for sperm accumulation. **B.** Sperm availability over time, when  
248 mating with a single female while maintaining the proportion  $\rho$  of  $s_{max}$  in reserve at each mating  
249 time. **C.** Sperm availability over time, when a male alternates regular mating with two females,  
250 each at frequency  $\mu$ ; his interval between mating bouts is  $1/(2\mu)$ . We assume that no reserves are  
251 retained in this case.

252

253 Overall, mating rate influences the advantage or disadvantage to a male of having a  
254 second mate through the implications for gamete availability and fertilization efficiency. Other  
255 influences on the optimal number of mates arise from benefits of male help at the nest and costs  
256 of mating, as noted in the next section.

## 257 Fitness

258 For simplicity and clarity, we assume that both partners' reproductive success is  
259 determined during the mating interval  $\tau$  and that fitness is maximized when reproductive success  
260 during  $\tau$  is maximized, as is typical in semelparous species (Bell, 1980). Note that fitness  
261 maximization would still hold for the male with subsequent partnering, if the same conditions  
262 apply to each partnership.

263 When the male has a single mate, eggs are fertilized at the efficiency  $\lambda_1$ , obtained by  
264 substituting  $E$  (from equation (2)) and  $S_1$  (from equation (3) or (5), depending on the mode of  
265 sperm production) into equation (1). Incorporating the total number of eggs released  $\varepsilon$  and the  
266 time interval  $\tau$  during which these are released produces an overall single-mate fertilization rate  
267 of  $\lambda_1\varepsilon/\tau$ . Similarly, when the male has 2 mates,  $S_2$  (from equation (4) or (6)) is substituted into  
268 equation (1) to obtain  $\lambda_2$ , yielding a 2-mate fertilization rate of  $\lambda_2\varepsilon/\tau$ . Figure 1 illustrates how the



269 parameters and key variables link mating to fitness (here, number of offspring successfully  
270 produced) for the two different types of sperm production: sperm recharge and a total stock of  
271 sperm set at maturation.

272         Suppose that a male with a single female mate provides more direct benefits (e.g. better  
273 care for fertilized eggs and developing offspring in the nest) than he could by attending two  
274 females. We express this additional increment of reproductive benefit per mate with one mate  
275 rather than two by the fitness multiplier  $\theta \geq 1$ . (This effect could instead be equivalently  
276 expressed as a cost, i.e. a reduction of care per mate when he attends two females, from having a  
277 second mate.) The features and implications of paternal care have been the focus of much  
278 research (Goldberg et al., 2020; Gross and Sargent, 1985; Stockley and Hobson, 2016), but for  
279 clarity here we must ignore these details and address only the net effect of dilutable benefits  
280 (Tazzyman et al., 2012), including care, and how male-provided benefits may increase through  
281 the fitness multiplier  $\theta$  with a single female mate rather than two.

282         Moreover, we express any fitness costs per mating, arising for example from physical  
283 damage to mates or enhanced predation risk (Daly, 1978; Parker, 1970b; Rowe, 1994) with  
284 negative exponential functions of the mating rate  $\mu$  and sex-specific coefficients  $c_f$  and  $c_m$ .  
285 Putting these features together, based on the total number of eggs  $\varepsilon$  provided by each female,  
286 allows us to express male and female fitness  $F$  via expected total offspring production over the  
287 reproductive interval  $\tau$ , depending on the number of females attended by the male, as

$$288 \quad F_{f1} = \theta \varepsilon \lambda_1 e^{-c_f \mu}, \quad (7)$$

$$289 \quad F_{m1} = \theta \varepsilon \lambda_1 e^{-c_m \mu},$$

$$290 \quad F_{f2} = \varepsilon \lambda_2 e^{-c_f \mu}, \text{ and}$$

291  $F_{m2} = 2\varepsilon\lambda_2 e^{-2c_m\mu},$

292 where the subscripts of fitness indicate the relevant sex and the number of females attended by  
293 the male.

294 We now have the fitness functions for each sex corresponding to one or two female mates  
295 per male, based on fertilization efficiency, egg number, male-provided dilutable benefits, and  
296 mating costs. These functions provide a basis for each mate to achieve the best mating rate  
297 contingent on the other mate's preference.

### 298 Solving the Game Between Mates

299 The result is a game to resolve the sexual conflict between mates, which we solve under  
300 the assumption that the mates can accurately predict their own and their partner's (or partners')  
301 costs and benefits in relation to mating rate. In the special case when  $\beta > 0$  and thus females  
302 occasionally withhold eggs, we assume that both partners behave as if they know the magnitude  
303 of  $\beta$ , but males are unaware of egg withholding in any particular instance (Petersson and Järvi,  
304 2001; Yamazaki and Koizumi, 2017). For example, physiological and environmental cues may  
305 inform females of  $\varepsilon$  and  $\tau$ , whereas males may estimate them from female body size and  
306 environmental cues. The partners may respond to a male's  $\theta$  and  $\gamma$ ,  $\sigma$ , or  $s_{max}$  based on his body  
307 size and environmental cues. The parameter  $\phi$  may tend to be relatively independent of body  
308 sizes and environment. Mating costs, linked to increased predation and disease risk or energetic  
309 expenditure, may be partly determined by observable body size and environmental conditions.  
310 We assume that the mates use heuristics (Gigerenzer et al., 2011) to integrate these data and their  
311 implications for the fitness functions and thus their decision making. An implication of this line

312 of thinking is that the responses should be plastic, depending for example on body sizes (e.g.  $\varepsilon$ ,  $\theta$ ,  
313  $\sigma$ ,  $s_{max}$ ,  $\gamma$ ,  $c_f$ ,  $c_m$ ,  $\mu_{max}$ ) and mortality risk ( $\tau$ ,  $c_f$ ,  $c_m$ ).

314           The game between mates can be resolved by considering the relationships among these  
315 fitness functions in response to adjustments in mating frequencies, as we illustrate graphically.  
316 The logic resulting in solutions of these games between mates is summarized in Appendix A.  
317 This is based on the game theoretic perspective that each mate acts to maximize their own fitness  
318 subject to constraints imposed by the partner seeking its own fitness maximization. To put this  
319 more formally but without the need for mathematics, we identify evolutionarily stable (ESS)  
320 strategies that correspond here to sex-specific strong Nash equilibria (Mesterton-Gibbons, 2000;  
321 Weibull, 1995): mating rates from which neither sex can shift and improve its fitness under the  
322 constraints imposed by the other sex. In particular, although the mating rate that maximizes male  
323 and female fitnesses may differ, neither male nor female can force its partner to mate. However,  
324 the female can decide to desert the nest and seek another mate if her partner chooses instead to  
325 obtain a second mate when this generates a severe cost to the female. Because mating rate, the  
326 sole evolving variable, is continuous and unimodally related to fitness, the ESS strategies are  
327 pure—no mixed strategies are possible. To evaluate the sensitivity of results to the model's  
328 parameter magnitudes, we determine the resulting mating rates and fertilization efficiencies  
329 across ranges of magnitudes of each parameter, placing the results less central to our questions of  
330 interest in Appendix B.

331

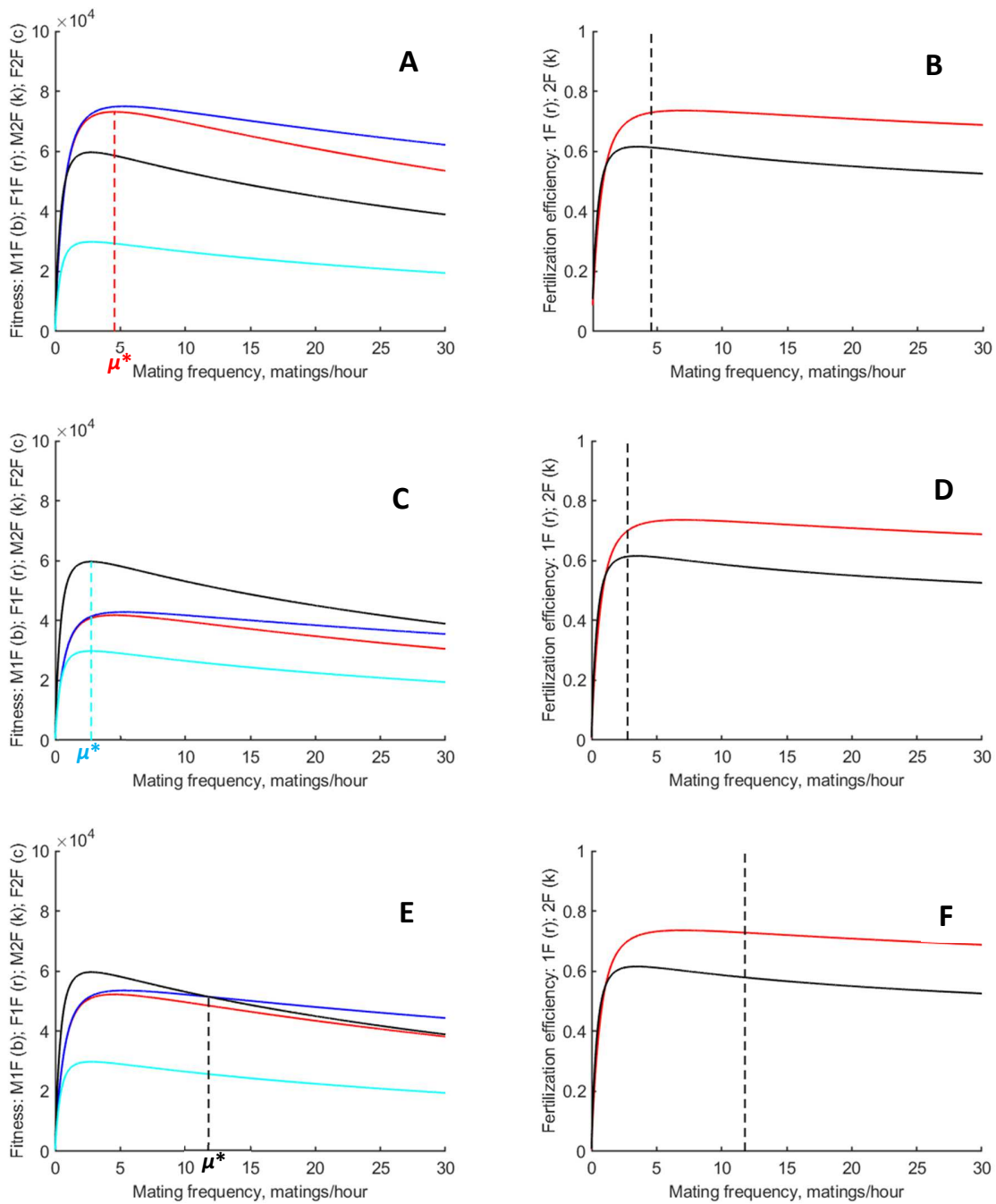
332

## Results

333           We summarize the results in the following sections by answering the four questions  
334 posed in the Introduction.

335 How can sexual conflict over within-pair mating rate be resolved for external fertilizers?

336           In this section, we focus on the results for sperm recharge to characterize and compare  
337 examples of the three outcomes that emerge across the full range of parameter magnitudes  
338 (Figure 3). These are found by comparing the fitness curves for a male with a single mate (blue  
339 lines), a female whose mate has no other female (red lines), a male with two female mates (black  
340 lines), and a female whose mate has a second mate (cyan lines). Corresponding fertilization  
341 efficiencies are for males with one mate (red lines) or two mates (black lines). We assume that  
342 each sex will attempt to choose the mating pattern and mating rate that maximize their fitness  
343 except when constrained by the choice of the other sex.



344

345 Figure 3 Fitness and fertilization efficiency as functions of mating frequency in 3 examples,  
 346 when sperm are recharged continuously. All parameter magnitudes are as in Table 1 except as  
 347 specified. Blue lines (b) in left-hand panels are male fitness and red lines (r) indicate female

348 fitness when the male is mating with a single female. The black line (k) is the male fitness when  
349 he is mating with two females; the cyan line (c) shows the female's fitness in that case.  
350 Fertilization efficiencies (right-hand panels) are shown for when the male mates a single female  
351 (red line, r) vs 2 females (black line, k). In panels **A** and **B**, the male fitness multiplier  $\theta = 2.1$ .  
352 Both the male and female maximize their fitness with a single mate, which results in consensus  
353 monogamy, *outcome 1*. **A** Male and female fitness are indicated by the red dashed line, where  
354 females maximize their fitness at  $\mu^*$ . **B** Fertilization efficiencies are maximized near the optimal  
355 mating rate. Unsurprisingly, the efficiency is consistently higher for a male with one mate than  
356 for a male with two. **C**. In this case, the male fitness multiplier  $\theta = 1.2$ . The male is always better  
357 off with a second female, which is the female's only option. Both fitness curves of the  
358 polygynous male (black) and his mate (cyan) are maximized at  $\mu^*$ , corresponding to the vertical  
359 cyan line. This pattern is polygyny, *outcome 2*. **D**. As in **B**, with very similar efficiencies. **E**.  
360 Here, the male fitness multiplier  $\theta = 1.5$ , the default magnitude. The negotiated settlement is a  
361 mating frequency just above the black dashed line, indicating where blue and black lines  
362 intersect at  $\mu^*$ . The male is restricted to a single mate. This pattern is referred to here as  
363 negotiated monogamy, *outcome 3*. **F**. Efficiencies are very similar to those in **B** and **D**.

364

365 The first outcome, which we refer to as “consensus monogamy”, or *outcome 1*,  
366 corresponds to a situation where the male benefitted from having a single mate at all mating  
367 frequencies, involving no conflict between mates over sperm allocation to an additional female.  
368 In this situation (Figure 3A), male and female fitness peak near the same mating rate. In this  
369 example we assume that females could maximize their fitness instead of the male's; their slightly  
370 lower optimal mating rate than that of males resulted from higher mating costs under our

371 assumed standard parameter magnitudes, and a lower mating rate is easily enforced by slowing  
372 down the mating process (see Appendix A), allowing female preference to dominate (red dashed  
373 line). Fertilization efficiencies (Figure 3B) are moderately high but higher for the male with a  
374 single mate.

375 The second outcome, we refer to as “polygyny”, or *outcome 2*. Outcome 2 resulted when  
376 the male was always better off with a second female, and females had no way of negotiating a  
377 better deal (Figure 3C). The male and female fitness maxima coincided at the vertical dashed  
378 cyan line. Any possibility of outcome 3 (see below) was precluded by the upper limit on mating  
379 rate  $\mu_{max}$ . The female’s only recourse in this case is to attempt to drive her rival away  
380 (Wittenberger and Tilson, 1980), which the male might try to prevent; we ignored these potential  
381 aggressive dynamics in the present analysis. Fertilization efficiencies (Figure 3D) were very  
382 similar to those for outcome 1. This is because the male fertilizes about the same number of eggs  
383 per mating bout with each female at the lower optimal mating rate with slightly more sperm  
384 released per bout (none held in reserve).

385 The third outcome, which we refer to as “negotiated monogamy”, or *outcome 3*, is  
386 depicted in Figure 3E. In this case, the male benefited from having a second mate below a  
387 pivotal mating frequency  $\mu^*$ , above which he was better off with a single mate. Because the  
388 female’s fitness was much lower regardless of mating rate if she shared her mate, she would  
389 solicit mating from the male (Briskie, 1992; as often observed; Hatch, 1987; Hatchwell and  
390 Davies, 1992) to a level just beyond the frequency at which he benefited from having a single  
391 mate. If the male would not mate that frequently, the female had a strong incentive to seek  
392 another mate to avoid the severe fitness cost of sharing, providing strong encouragement for the  
393 male to go along. Thus, the negotiated mating frequency was just above that at the pivotal

394 frequency; fitness declined for mates above this cutoff, eliminating any incentive to mate more  
395 frequently. Fertilization efficiencies (Figure 3F) were similar to those for the other two  
396 outcomes, here based on the higher mating rate at  $\mu^*$ .

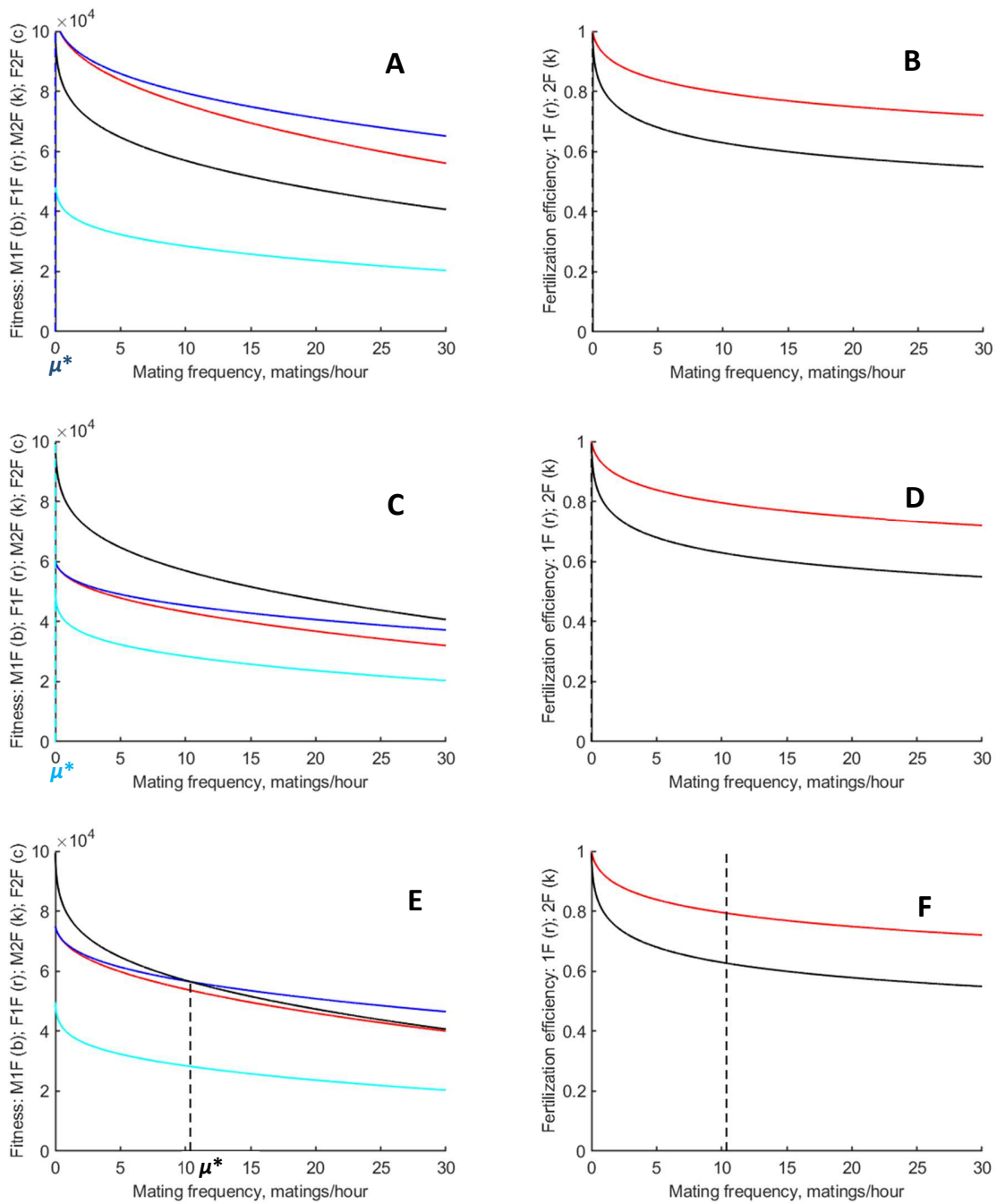
397 In Figure 3, the three different outcomes resulted from different magnitudes of the fitness  
398 coefficient accounting for male help at the nest, which we address in more detail below. With  
399 increasing magnitude of each parameter of the model (Table 1), the outcomes appear in the  
400 sequence 1 -> 3 -> 2 for the parameters  $x$  (egg number exponent),  $s_{max}$  (maximum recharged  
401 sperm per mating bout),  $\phi$  (sperm:egg fertilization coefficient),  $\rho$  (sperm recharge reserve), and  $\tau$   
402 (reproductive interval duration); and the outcomes appear in the order 2 -> 3 -> 1 for parameters  
403  $\varepsilon$  (eggs per female),  $\beta$  (sham mating proportion),  $\gamma$  (sperm recharge production coefficient),  $\theta$   
404 (fitness multiplier for male help), and  $\mu_{max}$  (maximum possible mating rate). Outcomes are  
405 insensitive to the magnitudes of parameters  $c_f$  and  $c_m$  (mating cost coefficients for females and  
406 males, respectively). We illustrate these results in Appendix B.

407 How does this conflict resolution depend on whether or not males continually regenerate sperm?

408 We answer this question by comparing the examples in Figures 3 (sperm recharge) and 4  
409 (stocked sperm). The same three outcomes (Figures 4A, 4C, and 4E) in same sequence with  
410 respect to parameter magnitudes are found for stocked sperm as for sperm recharge, following  
411 the same logic in accounting for each outcome. Outcome 3 (negotiated monogamy) yields a  
412 similar mating rate  $\mu^*$  (Figure 4E vs 3E) but slightly higher fertilization efficiencies with stocked  
413 sperm relative to sperm recharge (Figure 4F vs 3F). A key distinction arises with the other two  
414 outcomes. In both outcome 1 (Figure 4A) and outcome 2 (Figure 4C), the optimal mating  
415 frequencies are shown as zero, which implies biologically that the highest fitness is achieved



416 with a single mating over the entire mating interval—in other words, fertilization of the female’s  
417 entire egg load happens all at once with all of the male’s sperm. The single mating bout (i.e. no  
418 repeated mating) maximizes fitness in this case because fertilization efficiency is maximized at  
419 the minimal mating rate, as a result of higher likelihood of sperm-to-egg contact for a given  
420 sperm:egg ratio with more eggs per mating bout. This negative relationship between efficiency  
421 and mating frequency results from a fertilization exponent  $x < 1$ , consistent with trend  
422 anticipated in the Methods. In contrast, sperm recharge results in a sharp decline in fertilization  
423 efficiency as the mating rate becomes very small, because sperm production per mating bout is  
424 constrained by the upper limit  $s_{max}$ , while egg number per bout increases with a declining mating  
425 frequency. This effect ensures that the optimal mating rate for any of the three outcomes is  
426 positive, generally implying multiple mating episodes, for sperm recharge.



427

428 **Figure 4** Fitness and fertilization efficiency as functions of mating frequency in 3 examples,  
 429 when the stock of sperm is set at maturation. All parameter magnitudes are as in Table 1 except  
 430 as specified. Blue lines (b) in left-hand panels are male fitness and red lines (r) indicate female  
 431 fitness when the male is mating with a single female. The black line (k) is the male fitness when

432 he is mating with two females; the cyan line (c) shows the female's fitness in that case.  
433 Fertilization efficiencies (right-hand panels) are shown for when the male mates a single female  
434 (red line) vs 2 females (black line). In, panels **A** and **B**, the male fitness multiplier  $\theta = 2.1$ . The  
435 male has a single mate. Male and female both maximize their fitness at  $\mu^* = 0$ . This pattern is  
436 consensus monogamy, *outcome 1*. **B**. Fertilization efficiency declines with increasing mating  
437 rate, because the fewer eggs per mating are fertilized less efficiently. **C** and **D**. Here, the male  
438 fitness multiplier  $\theta = 1.2$ . The male has a single mate.; the male is always better off with a  
439 second female, which is the female's only option. Both fitness curves are maximized at  $\mu^* = 0$ .  
440 This pattern is polygyny, *outcome 2*. The fertilization efficiencies here are similar to those in **B**.  
441 **E** and **F**. Here, the male fitness multiplier  $\theta = 1.5$ , the default magnitude. The negotiated  
442 settlement is a mating frequency just above the black dashed line, indicating where blue and  
443 black lines intersect at  $\mu^*$ . The male is restricted to a single mate. This is referred to negotiated  
444 monogamy, *outcome 3*. Fertilization efficiencies are very similar to those in **B** and **D**.

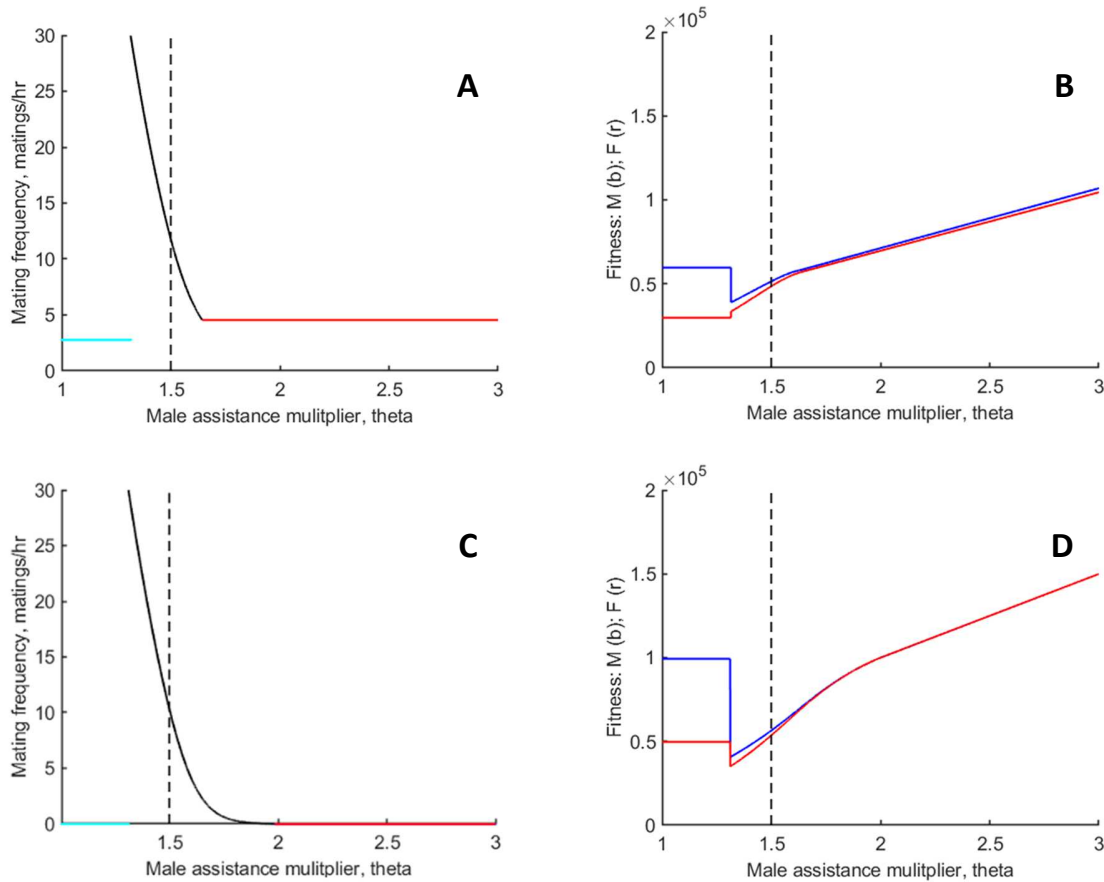
445

446 To summarize the key result, *for stocked sperm, only the negotiated mating frequency*  
447 *(outcome 3) allowed repeated within-pair mating, whereas with continuous recharge, fitnesses*  
448 *are always maximized at intermediate mating frequencies.*

449 How do the mating patterns depend on the dilutability of male-provided benefits?

450 With the parameter  $\theta$ , we represent the additional contribution to reproductive success in  
451 a nest that a male makes by restricting himself to a single mate, rather than two. Figure 5 shows  
452 how the mating rate, outcome, and fitness depend on the magnitude of  $\theta$ . With  $\theta = 1$ , there is no  
453 reproductive advantage per nest of the male's fidelity to one mate regardless of the sperm

454 production mechanism, and outcome 2 with the male attending two mates is the stable outcome  
455 (Figures 5A and 5C). For intermediate magnitudes of  $\theta$ , the result is outcome 3 (negotiated  
456 monogamy), with mating rate steeply declining for larger  $\theta$ . Magnitudes above about 1.65  
457 (sperm recharge, Figure 5A) or 1.9 (stocked sperm, Figure 5B), the result is outcome 1  
458 (consensus monogamy). Except in the zone of outcome 3, mating frequencies are low and  
459 independent of  $\theta$  (sperm recharge) or minimal (i.e. once for the female's entire egg load, stocked  
460 sperm). Fitnesses are constant within sex and differ in favor of males by about a factor of 2 in the  
461 outcome-2 zone, converging to nearly identical magnitudes for the other outcomes, with  
462 magnitudes rising from the increased levels of male help. Overall, the magnitude of male help  
463 and the extent to which this reproductive contribution can become diluted by a males's divided  
464 loyalties between females strongly influences the mating patterns expected to arise.



465

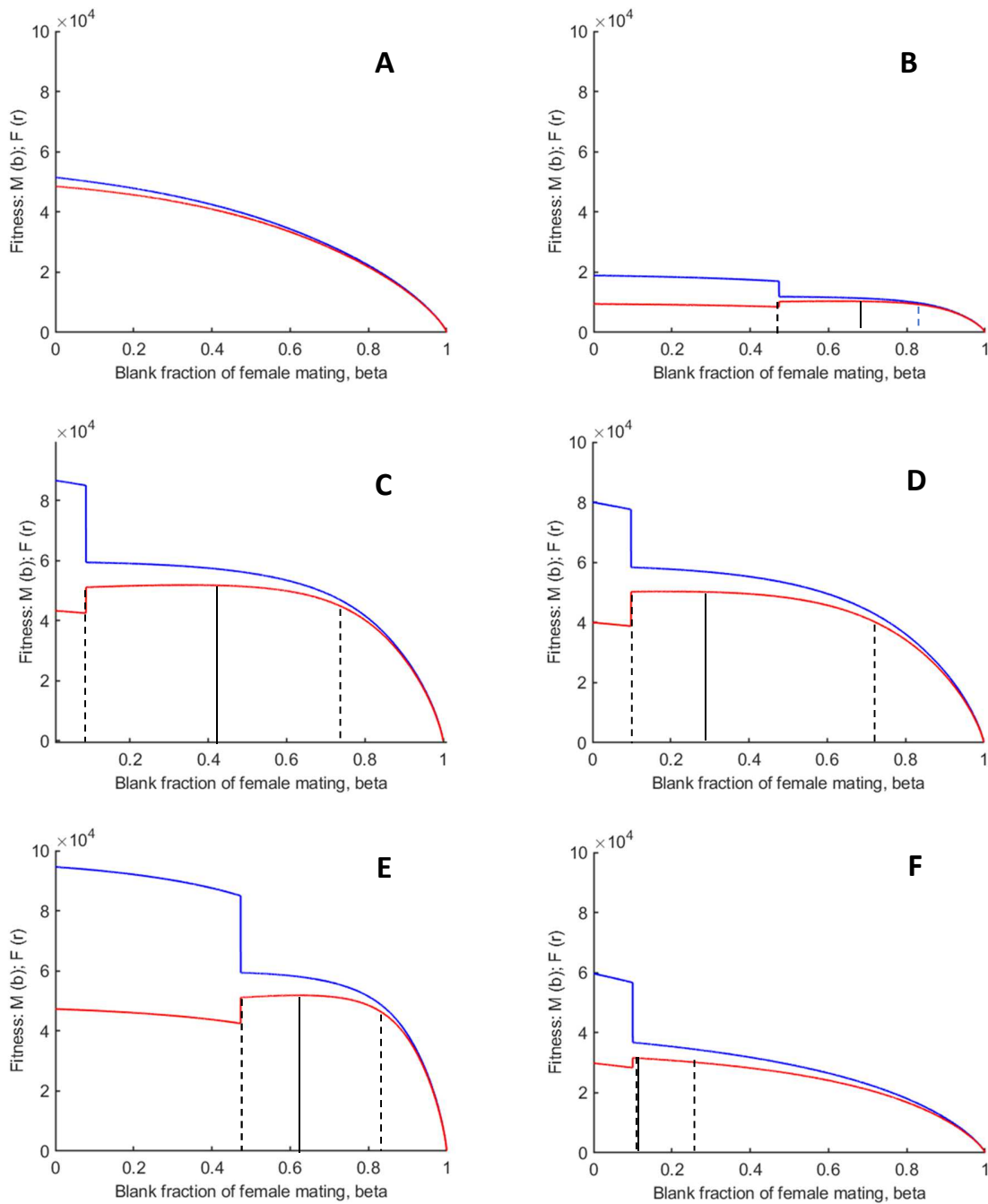
466 Figure 5 Mating frequencies and fitnesses over a range of the male fitness multiplier  $\theta$ . Vertical  
 467 dashed lines indicate default parameter magnitudes. In the mating frequency panels, red lines (r)  
 468 are outcome 1, cyan lines (c) are outcome 2, and black lines (k) correspond to outcome 3. In the  
 469 fitness panels, blue lines (b) are male fitness and red lines (r) are female fitness. **A** and **B**, the  
 470 sperm recharge case. **C** and **D**, stocked sperm.

471

472 Why might females sometimes withhold eggs during mating bouts?

473 Consider first the sperm recharge case. With default parameter magnitudes (Table 1),  
 474 females are better off not withholding eggs (Figure 6A, red line)—their highest fitness

475 corresponds to  $\beta = 0$ . However, changes in some of the parameter magnitudes yields magnitudes  
476 of  $\beta$  between 0 and 1 with higher female fitnesses than for  $\beta = 0$ . Figure 6 contains five examples  
477 with a range of  $\beta$  magnitudes producing increased female fitness. In each case, the relevant range  
478 of  $\beta$  is between a pair of vertical dashed lines on the figure, with the maximal-fitness magnitude  
479 of  $\beta$  indicated by a solid vertical line. These are for a total number of eggs per female  $\varepsilon = 10,000$   
480 (default  $\varepsilon = 50,000$ ) (Figure 6B); raising either the sperm:egg fertilization coefficient  $\phi$  from  
481 0.003 to 0.007 or the maximum sperm recharge  $s_{max}$  from 50,000 to 117,000 (Figure 6C);  
482 increasing the sperm production coefficient  $\gamma$  from 3 to 7 (Figure 6D); increasing the total  
483 reproductive interval duration  $\tau$  from 96 hours to 480 hours (Figure 6E); and decreasing the  
484 fitness multiplier for male help from 1.5 to 1.3 (Figure 6F).



485

486 **Figure 6** Fitnesses of males (blue lines) and females (red lines) vs the blank or withheld-fraction  
 487 of mating bouts  $\beta$  when eggs are not released by the female. Males engage in sperm recharge.  
 488 Vertical dashed lines bound the magnitudes of  $\beta$  where females are able to increase their fitness  
 489 relative to  $\beta = 0$  by withholding eggs at those frequencies. Solid vertical lines indicate the fitness

490 maximizing (optimal magnitude) of  $\beta$ . **A** All parameters are at default magnitudes (Table 1), and  
491 outcome 3 (negotiated monogamy) prevails over the whole range of  $\beta$ . In all other cases here, the  
492 patterns arise with outcome 2 (polygyny) at  $\beta = 0$ , shifting to outcome 3 at some higher  
493 magnitude of  $\beta$ . **B**: Total eggs per female  $\varepsilon = 10,000$ . **C** Either  $\phi = 0.007$  or  $s_{max} = 117,000$ . **D**  $\gamma =$   
494 7. **E**  $\tau = 480$ . **F**  $\theta = 1.3$ .

495

496 For stocked sperm, raising  $\beta$  above zero did not increase female fitness for any of the  
497 alternative magnitudes we checked of the male help coefficient  $\theta$  or the reproductive interval  
498 duration  $\tau$ . However, substantial increases in the female's egg load  $\varepsilon$  or the sperm:egg  
499 fertilization coefficient  $\phi$  did increase female fitness for ranges of  $\beta$  between 0 and 1, similar to  
500 sperm recharge.

501 These results show that optimal magnitudes of the frequency of egg-withholding by  
502 females during mating can in some cases exceed zero. So in some situations females may  
503 actually increase their own fitness by not releasing eggs in every mating bout.

504

505

## Discussion

506 In this analysis, we addressed the possibility that repeated within-pair mating could be a  
507 way to resolve the sexual conflict over fertilization efficiency and dilutable benefits in external  
508 fertilizers. We showed that repeated within-pair mating can be a mate guarding tactic used by  
509 females to manipulate males into monogyny through increased fertilization efficiency and  
510 increased benefits provided by males to their joint offspring. Despite mating costs that favor low  
511 mating frequency for some parameter values, other magnitudes (discussed below) allowed



512 females to raise mating frequency up to a level that secured monogamy. Under the default  
513 parameter values, based on lamprey reproductive biology, the ESS mating frequency reached 10  
514 matings per hour, similar to what is observed in these animals (Applegate, 1950; Malmqvist,  
515 1983; Manion and Hanson, 1980).

516         While repeated within-pair mating was initially thought to result from males trying to  
517 maximize their paternity share in the context of sperm competition (Møller et al., 1987), Petrie  
518 (1992) proposed that frequent copulation, possibly with solicitation, could be a way for a female  
519 to guard her mate by depleting his time, energy, sperm supply, and opportunities to mate with  
520 others. She predicted that females paired with high-quality males (providing more direct benefits,  
521 in the form of paternal care or territory quality) in species with more intense female-female  
522 competition for high-quality males should tend to solicit mating repeatedly (e.g. Davies et al.,  
523 1996; Saether et al., 2001). Likewise, females in such species are expected to solicit mating  
524 throughout the period when their mates can provide direct benefits, such as paternal care or  
525 territory quality (Doran-Sheeny et al., 2009; and possibly outside the fertile period; e.g. Wysocki  
526 and Halupka, 2004), and more intensively when the risk of extra-pair copulation or desertion is  
527 high (Davies et al., 1996; e.g. Eens and Pinxten, 1995; Sandell and Smith, 1996).

528         In place of the classical direct/indirect categorization for male-provided benefits  
529 (Andersson, 1994), we used the alternative concept of dilutable benefits proposed by Tazzyman  
530 et al. (2012). They emphasized that the distinction between fixed benefits whatever the number  
531 of mates and those that are dilutable among the male's mates could shape the form of female  
532 preference. Instead of a binary categorization, we modelled benefit dilutability as a continuous  
533 feature through the parameter  $\theta$ , which quantified the benefit to the offspring of a monogamous  
534 father relative to the offspring of a polygamous one. This quantitative approach showed that the

535 dilutability of benefits could affect the evolutionarily stable outcome (monogamy, polygyny,  
536 negotiated monogamy) and the mating rate at equilibrium (Figure 5). For example, when a male  
537 fish accommodates the eggs of all his mates in a single nest (Jones et al., 2001; Kraak et al.,  
538 1999), the size of the nest can set the dilutability of the benefits it provides: egg survival would  
539 depend less on the number of females which oviposited in it (*i.e.* less dilutable benefit) in a large  
540 nest than in a small nest. In such a system, our model predicts that negotiated monogamy and  
541 repeated mating should be found in nests of intermediate size, while monogamy and polygyny  
542 with low mating rate should be observed in small and large nests, respectively.

543         A central role in our model was played by gamete management from both the male and  
544 female perspective. Females of species with marked seasonal reproduction usually start the  
545 season with a finite stock of oocytes that may mature all at once or in batches, a feature known as  
546 determinate fecundity in fishes (Ganias et al., 2015) and pro-ovigeny in insects (particularly in  
547 parasitoids, Jervis et al., 2001). Moreover, females of externally fertilizing species can control  
548 the frequency with which they release their eggs to have them fertilized by their mates' sperm  
549 during mating (Kiflawi, 2000; Shapiro and Giraldeau, 1996). They can also occasionally  
550 withhold eggs despite adopting the usual mating posture that in this case triggers ineffective  
551 ejaculation (Jones and Ball, 1954; Esteve, 2007; Schneider, 1971; Ridgway et al., 1989; Roy and  
552 Pal, 1986; Yamazaki and Koizumi, 2017; Petersson and Järvi, 2001). This deceptive behavior  
553 can be quite frequent, reaching for example 65% of matings in the Arctic lamprey (Yamazaki  
554 and Koizumi, 2017). Outcome 3 (negotiated monogamy), emerging under some magnitudes of  
555 our model's parameters, indicates that females may adjust their rate of egg release, and hence the  
556 rate of within-pair mating. This can maximize female fitness based on the sperm supplied and the  
557 dilutable male-provided benefits. We also showed that under some conditions, withholding eggs

558 for a substantial proportion of matings could be adaptive for the females because all other  
559 parameters being equal, it could result in a shift from polygyny to negotiated monogamy and an  
560 associated increase in female fitness. The proportion of eggs withheld having a quite weak effect  
561 on female fitness (flat curve around optimum in Figure 6) and a negative effect on male fitness,  
562 one could expect males to evolve counteradaptations. However, efficient external fertilization  
563 often requires males to ejaculate synchronously or even slightly before egg release, especially  
564 under sperm competition (Fitzpatrick and Liley, 2008; Yeates et al., 2007), despite the risk of  
565 getting tricked by females. Our model indicates that egg withholding could favor the evolution of  
566 mating rate as a male-guarding strategy in females, but the probability of withholding ( $\beta$ ) was  
567 not allowed to evolve. On the other hand, we suggest that future attempts to understand the  
568 evolution of egg withholding in external fertilizers should account for its possible role as a mate  
569 guarding strategy.

570         The male-female settlement on mating rate obtained under outcome 3 resembles the logic  
571 of reproductive skew (e.g. see Buston and Zink, 2009), except that the negotiations here are  
572 between sexes rather than within sex. As in transactional models of reproductive skew, where a  
573 dominant individual grants just enough reproduction to group members so that they benefit more  
574 by staying and helping than by leaving, here the female ensures a mating rate just sufficient to  
575 incentivize the male to stay, and to secure exclusive access to dilutable benefits. In transactional  
576 models of reproductive skew, the access of subordinates to reproduction is limited to what the  
577 dominant consents to give. Yet one subtlety of our model arises from physiological processes  
578 such as sperm recharge rate or amount of stored sperm that impose a limit on the staying  
579 incentives the male can accept from the female. Sperm management, and in particular the  
580 dynamics of spermatogenesis, had major effects on the evolutionarily stable outcome of the

581 sexual conflict addressed by our model. First, repeated within-pair mating was predicted to some  
582 extent under all three outcomes (1: consensus monogamy, 2: polygyny, 3: negotiated  
583 monogamy) when sperm was recharged after ejaculation, whereas it was predicted to occur only  
584 under negotiated monogamy in the case of finite stock (Figures 3-4). Second, within each  
585 scenario of spermatogenesis, parameters pertaining either to the maximum sperm storage, to the  
586 reserve held at each ejaculation, or to the rate of sperm production affected the outcome (1, 2 or  
587 3) and the mating rate (see Appendix B).

588 Interspecific variation exists in the dynamics of sperm stocking, with males of many  
589 species being able to recharge their sperm stock during a refractory period (Dewsbury, 1982),  
590 and males of other species relying on a finite sperm stock once mature (Boivin et al., 2005;  
591 Docker et al., 2019; Michalik and Lipke, 2013; Wootton and Smith, 2014). Within species,  
592 interindividual variation is observed either in the maximum sperm storage or in the rate of  
593 recharge (O’Dea et al., 2014), and selection could operate on this variability, especially when  
594 sperm limitation impacts a male's fitness (Dewsbury, 1982). Nevertheless, most models of  
595 gamete management focus on gamete release (so-called ejaculate economics) without explicitly  
596 representing the dynamics of gamete synthesis, whether the stake is fertilization efficiency in  
597 external fertilizers without sperm competition (Kiflawi, 2000; Shapiro and Giraldeau, 1996) or  
598 sperm competition in polyandrous internal fertilizers (Parker and Pizzari, 2010; Wedell et al.,  
599 2002). Our results suggest that repeated within-pair mating should be observed in species where  
600 males recharge their sperm only under conditions favoring negotiated monogamy, and that  
601 female repeated solicitation for mating should coevolve with rapid sperm recharge.

602 Our model focused on polygyny and did not consider polyandry or polygynandry, despite  
603 the "polyandry revolution" (Parker and Birkhead, 2013; Pizzari and Wedell, 2013) initiated by

604 Parker (1970a). Our point is not to downplay the major role of sperm competition in the  
605 evolution of mating behavior (although external fertilizers may be less exposed to sperm  
606 competition; Fitzpatrick, 2020), but to identify another process which may be at play. Many  
607 models of gamete allocation exist in the context of polygynandry (Parker and Pizzari, 2010;  
608 Wedell et al., 2002), some of which allow gamete allocation among matings to evolve in both  
609 males and females (Abe and Kamimura, 2015; Alonzo and Pizzari, 2013). These models address  
610 multiple mating without explicitly distinguishing between mating with multiple partners and  
611 repeated within-pair mating. But repeated within-pair mating could also be a way for  
612 polyandrous females to express male preference (Andrade and Mason, 2000; Simmons, 1987) or  
613 to limit harassment by other males (Wysocki and Halupka, 2004). Theoretical work  
614 incorporating sperm competition to the kind of model described here would therefore be a further  
615 step toward the understanding how sexual conflicts over mating rate are resolved.

616

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621

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625

626

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806

807 Appendix A. Logic resulting in solutions to the games between mates

808 There are three possible qualitatively different outcomes (1, 2, and 3), based on the four  
809 mating-frequency-related fitness magnitudes (the fitness of a male with one mate [M-1], a male  
810 with two mates [M-2], a female when her mate has no other mate [F-1], and a female when her  
811 mate has an additional mate [F-2]). The circumstances in which each outcome arises are as  
812 follows:

813 1: Consensus monogamy. Here the male or the female can maximize fitness—whichever has the  
814 lower optimal mating frequency. This requires that M-1 and F-1 are greater than M-2 and F-2  
815 across the entire possible range of mating rates. Because either mate can slow the mating rate in  
816 the absence of forced mating, the sex with the lower optimum will prevail—which amounts to  
817 manipulation rather than negotiation to achieve an evolutionarily stable mating rate that neither  
818 sex can improve on.

819 2: Polygyny. When M-2 exceeds M-1 for all mating frequencies, the male will attempt to obtain  
820 and retain a second mate, and the first female has no recourse. This evolutionarily stable  
821 outcome generally requires a fertilization efficiency almost as high for each female in the two-  
822 mate case as for a single mate. In the present analysis, we assume that the second mate is readily  
823 available when desired, but in nature a lag before a second mate can be acquired benefits the first  
824 mate. In this case, one female strategy might be to stay with a male only until a second mate  
825 arrives, a possibility we do not pursue further here. Whether this could provide sufficient  
826 protection for the eggs already released would depend on the particular circumstances.

827 3: Negotiated monogamy. There is some mating frequency at which M-1 = M-2. In this case,  
828 letting the mating rate of equality be  $\mu^*$ ,  $\frac{dF_{m2}}{d\mu} < \frac{dF_{m1}}{d\mu}$  at  $\mu^*$ , with both slopes negative. The



829 intersection requires that male fitness is higher with two females than with one at low mating  
830 rates because of efficient use of sperm; but fitness is lower with two females than with one at  
831 high mating rates because of less efficient sperm use. In this case, females need to avoid sharing  
832 their mate with an additional female, because  $F-2$  is generally much lower than  $F-1$ . Females  
833 seeking to accomplish this may solicit mating. Males will comply because in this situation  
834 females will avoid or abandon males with a second female. The compromise reached at  $M-1 =$   
835  $M-2$  can be considered the result of “negotiation”. This is an evolutionarily stable outcome,  
836 because neither male nor female can increase fitness by imposing a different mating rate.

837

838

## Appendix B. Additional Analysis of Parameter Effects

839 Mating rates and outcomes across plausible ranges of all parameters from Table 1 (except  
840  $\theta$ , for which mating rates were explored in text Figure 5) are presented here in Figures B1-B4.  
841 Figures B1 and B2 report results for sperm recharge; Figures B3 and B4 are for stocked sperm.  
842 Vertical dashed lines indicate default parameter magnitudes. Red lines (r) are outcome 1, cyan  
843 lines (c) are outcome 2, and black lines (k) are outcome 3. These are intended in part as a  
844 sensitivity analysis, from which we conclude that mating rates for both types of sperm  
845 production are very strongly sensitive to the magnitude of  $\theta$  (text Figure 5 and Figure B4-B),  
846 strongly sensitive to the magnitudes of the parameters  $\varepsilon$ ,  $x$ ,  $s_{max}$ ,  $\phi$ ,  $\gamma$ ,  $\rho$ ,  $\tau$  (for sperm recharge, but  
847 only moderately sensitive for stocked sperm), and  $c_m$ , moderately sensitive to  $\beta$ , and incentive to  
848  $\mu_{max}$  and  $c_f$ . This overall pattern suggests that mating rates may respond extensively to the  
849 physiological and ecological features that can influence parameter magnitudes under a given set  
850 of conditions. Particular attention must be paid to understanding how the relative contributions  
851 from male help  $\theta$  may be expressed depending on whether the male is able to retain a second  
852 mate. Outcomes are generally much less sensitive to parameter magnitudes, especially for  
853 stocked sperm, but again with  $\theta$  as an exception.

854

855

Figure legends for Appendix B

856 Figure B-1 Mating frequencies and fitnesses over ranges of parameter magnitudes, with  
857 continuous sperm recharge. Vertical dashed lines indicate default parameter magnitudes. In the  
858 mating frequency panels, black lines correspond to outcome 0, red lines are outcome 1, and cyan  
859 lines are outcome 2. In the fitness panels, blue lines are male fitness and red lines are female  
860 fitness. **A** Total eggs per female,  $\varepsilon$ . **B** Fertilization exponent,  $x$ . **C**: Maximum sperm storage,  $s_{max}$ .  
861 **D** Fertilization efficiency coefficient,  $\phi$ . **E**: Sperm production coefficient,  $\gamma$ . **F** Blank (sham)  
862 fraction of female mating,  $\beta$ .

863 Figure B-2 Mating frequencies and fitnesses over ranges of parameter magnitudes, with  
864 continuous sperm recharge. Vertical dashed lines indicate default parameter magnitudes. In the  
865 mating frequency panels, black lines correspond to outcome 0, and cyan lines are outcome 2. In  
866 the fitness panels, blue lines are male fitness and red lines are female fitness. **A** Sperm reserve,  $\rho$ .  
867 **B** Expected reproductive lifetime,  $\tau$ . **C** Female mating cost,  $c_f$ . **D**. Male mating cost,  $c_m$ . **E**  
868 Maximum mating rate,  $\mu_{max}$ .

869 Figure B-3 Mating frequencies and fitnesses over ranges of parameter magnitudes, with sperm  
870 stocked at maturation. Vertical dashed lines indicate default parameter magnitudes. In the mating  
871 frequency panels, black lines correspond to outcome 0, red lines are outcome 1, and cyan lines  
872 are outcome 2. In the fitness panels, blue lines are male fitness and red lines are female fitness. **A**  
873 Total eggs per female,  $\varepsilon$ . **B** Fertilization exponent,  $x$ . **C** Total sperm per male,  $\sigma$ . **D** The  
874 fertilization efficiency coefficient,  $\phi$ . **E** Sperm reserve,  $\rho$ . **F** Blank (sham) fraction of female  
875 mating,  $\beta$ .

876 Figure B-4 Mating frequencies and fitnesses over ranges of parameter magnitudes, with sperm  
877 stocked at maturation. Vertical dashed lines indicate default parameter magnitudes. In the mating  
878 frequency panels, black lines correspond to outcome 0, red lines are outcome 1, and cyan lines  
879 are outcome 2. In the fitness panels, blue lines are male fitness and red lines are female fitness. **A**  
880 Expected reproductive lifetime,  $\tau$ . **B** Male assistance multiplier,  $\theta$ . **C** Female mating cost,  $c_f$ . **D**  
881 Male mating cost,  $c_m$ . **E** Maximal mating rate,  $\mu_{max}$ .

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Figures from Appendix B

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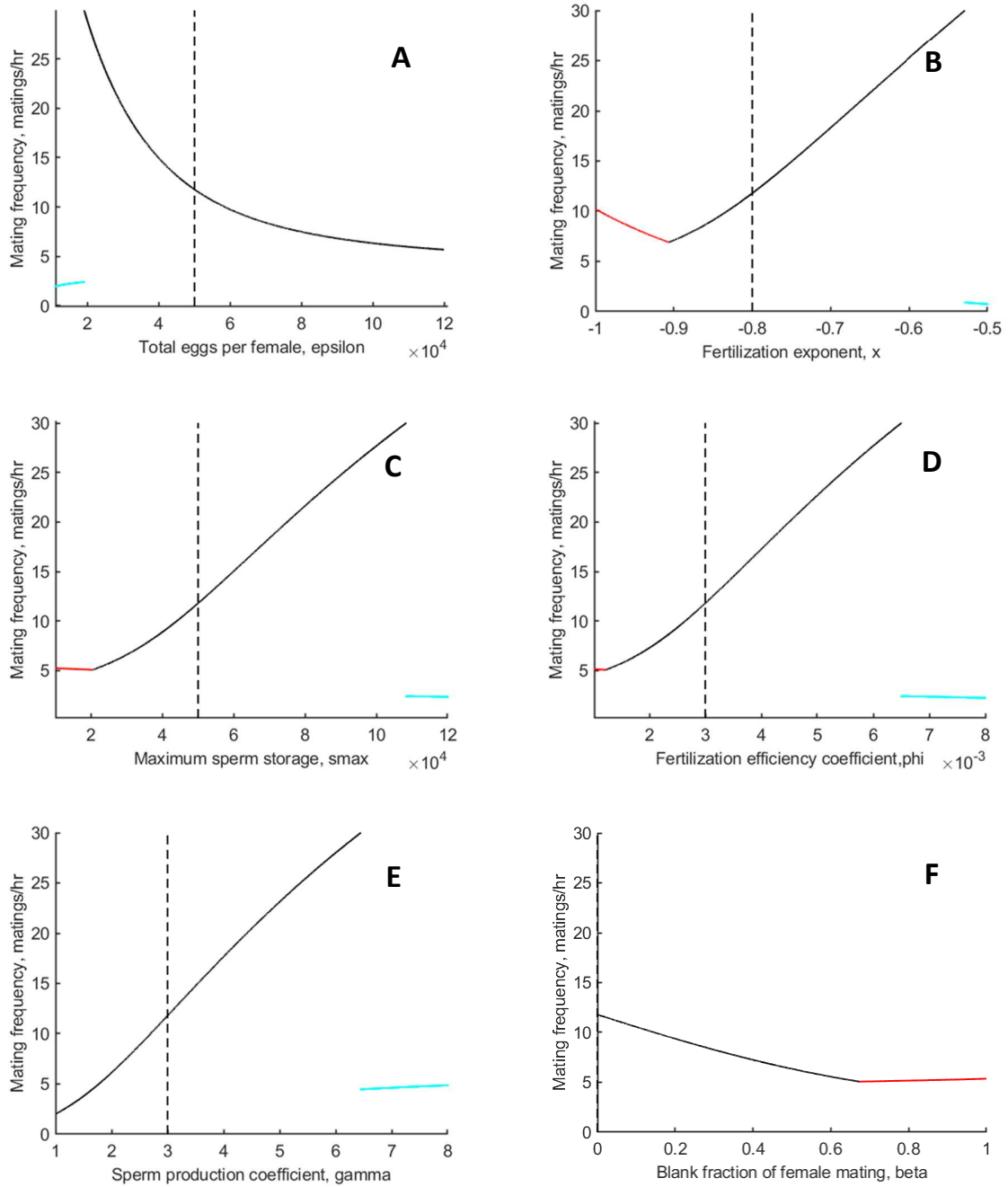


Figure B1

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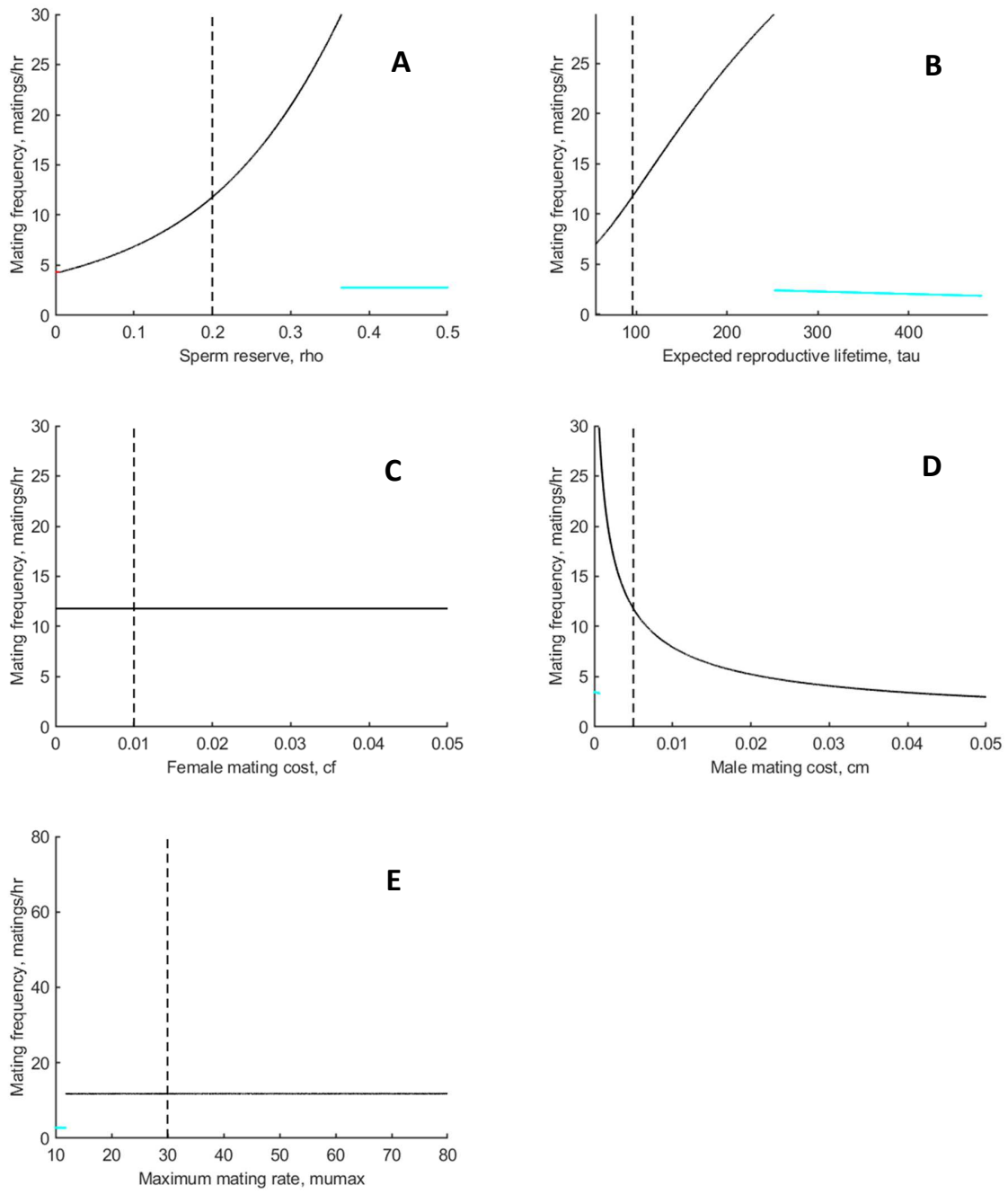


Figure B2

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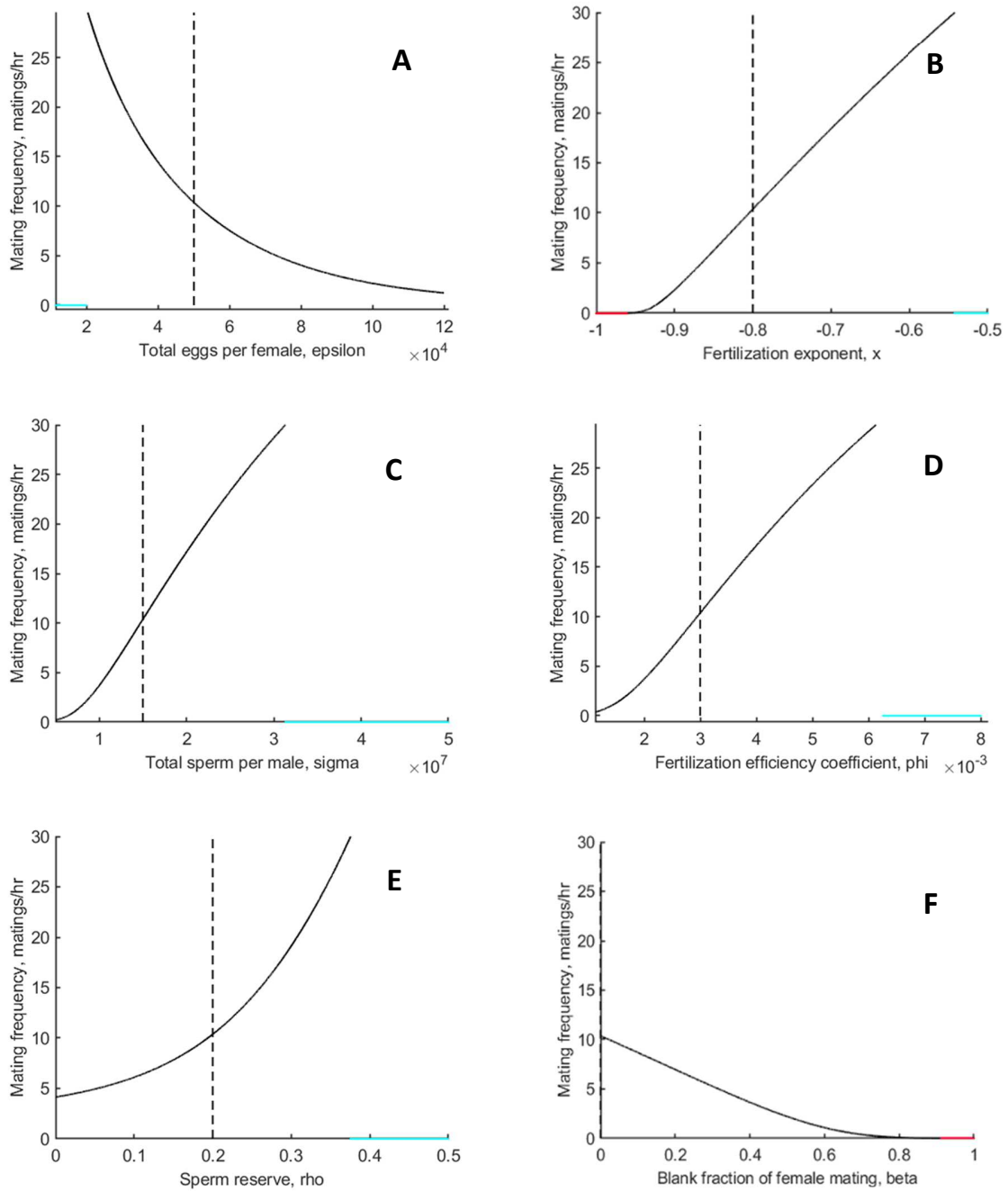


Figure B3

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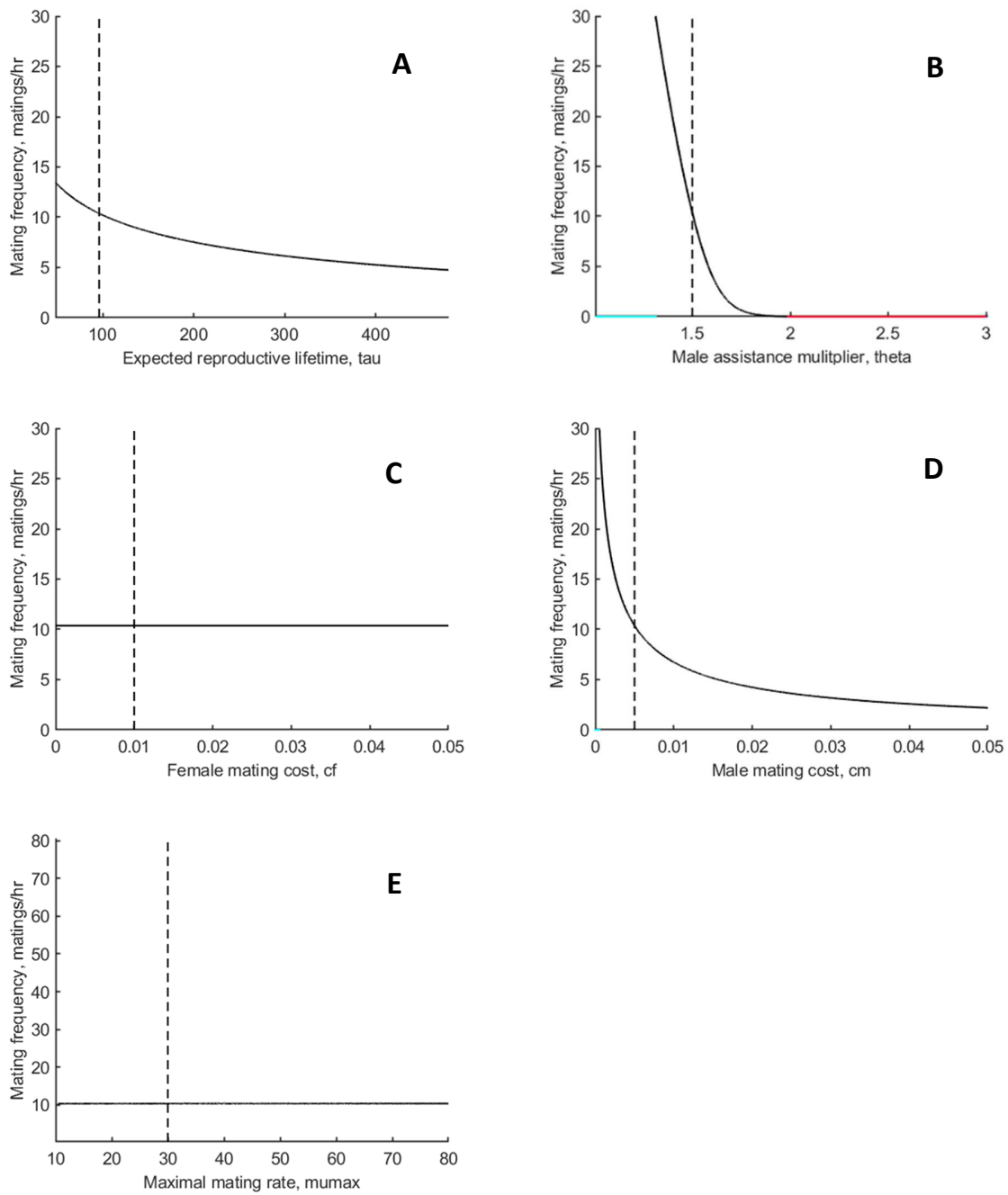


Figure B4