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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


#### Abstract

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


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

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

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

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

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

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

Our goal is therefore to predict how gamete management affects the resolution of malefemale conflict over mating rate in external fertilizers with no sperm competition but with maleprovided benefits (i.e. to build a "resolution" model, sensu Parker, 2006). To do this, we derive and analyze a simple game theoretic model based on finding the ESS mating rate for a single mating season and the use of all available gametes, nest building, and external fertilization (Figure 1), from which we derive the expected mating patterns. This enables us to address the following four questions:
(1) How can sexual conflict over within-pair mating rate be resolved for external fertilizers?
(2) How does this resolution depend on whether or not males continually regenerate sperm?
(3) How do the mating patterns depend on the efficacy of male help at the nest?
(4) Why might females sometimes withhold eggs during mating bouts?


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

Methods

As a biological grounding for the derivation, we envision an externally fertilizing, semelparous, nest building, pair bonding species, such as many fishes (Wootton and Smith, 2014). Our model is deterministic, using fixed parameter magnitudes to obtain what can be
considered expectations from an underlying stochastic formulation. We emphasize that a stochastic version of the dynamics we depict may yield somewhat different results.

We begin by assuming that constant numbers of eggs and sperm, specifically $E$ and $S$, are released by mates in each mating bout. We assume that the ratio of sperm released to eggs released during a mating bout determines the fertilization efficiency $\lambda$, but with two important caveats. (1) A larger number of eggs released by a mating female should generally provide a denser target for sperm to encounter them more efficiently; in other words, each individual sperm has a chance of encountering an egg that increases per egg with greater numbers of eggs released (Vogel et al., 1982). We represent this effect in the sperm-to-egg ratio by raising the number of eggs $E$ to the power $x$, where $0<x \leq 1$. (2) Fertilization efficiency $\lambda$ should increase with the sperm-to-egg ratio (as modified in caveat (1)) but with diminishing returns, so that very high ratios approach the maximum efficiency of 1 (Lehtonen and Dardare, 2019). We represent this effect with the exponential function
$\lambda=1-e^{-\varnothing\left(\frac{S}{E^{x}}\right)}=1-e^{-\varnothing S E^{-x}}$,
where $\varnothing$ is the coefficient determining how rapidly the efficiency approaches its upper limit with increasing sperm-to-egg ratio. See Table 1 for a list of all model parameters, definitions, standard or default magnitudes, and units.

Table 1. Parameters of the Model

| $\underline{\text { Symbol }}$ | Definition | $\underline{\text { Magnitude }}$ a | Units |
| :--- | :--- | :--- | :--- |
| $\varepsilon$ | Total number of eggs per female | 50,000 | eggs |


| $x$ | Egg number exponent for fertilization efficiency | 0.8 | dimensionless |
| :--- | :--- | :--- | :--- |
| $\beta$ | Proportion of matings with no eggs released | 0 | dimensionless |
| $\sigma$ | Total number of sperm per male (stocked sperm) | $1.5 \times 10^{7}$ | sperm |
| $s_{\text {max }}$ | Maximum recharged sperm per mating bout | 50,000 | sperm |
| $\phi$ | Sperm:egg saturation coefficient for fertilization | 0.003 | per-bout sperm ${ }^{-1}{ }^{\text {eggs }}{ }^{x}$ |
| $\gamma$ | Sperm production coefficient (sperm recharge) | 3 | matings/hour |
| $\rho$ | Sperm reserve proportion (sperm recharge) | 0.2 | dimensionless |
| $\tau$ | Total duration of the reproductive interval | 96 | hours |
| $\theta$ | Fitness multiplier accounting for male help | 1.5 | dimensionless |
| $c_{f}$ | Fitness cost coefficient for a female per mating | 0.01 | hours/mating |
| $c_{m}$ | Fitness cost coefficient for a male per mating | 0.005 | hours/mating |
| $\mu_{m a x}$ | Maximum possible mating rate | 30 | matings/hour |

during mating events. We assume that she spends the duration $\tau$ of her reproductive interval with a single male partner. With the help of this partner, she constructs and maintains a nest where eggs are released, fertilized, tended, and protected to benefit their survival and initial development. We assume that mating happens at some consistent frequency $\mu$ to use up all eggs during $\tau$, which would imply the release of $E=\varepsilon /(\mu \tau)$ eggs at each mating. However, we also allow for the possibility that females fail to release any eggs in the proportion $\beta$ of matings, as documented in some fishes (Esteve, 2007; Jones and Ball, 1954; Ridgway et al., 1989; Roy and Pal, 1986; Schneider, 1971; Yamazaki and Koizumi, 2017). As a result, the number of eggs released when eggs are not withheld, $E$, would need to be
$E=\varepsilon /((1-\beta) \mu \tau)$,
so that all eggs are released during time $\tau$. To address whether egg withholding could be beneficial to the female (question 4 in the introduction), we assessed the effect of variation in $\beta$ on the mating rate at equilibrium and on fitness. However, for the sake of simplicity, $\beta$ was not allowed to evolve in the model, and the mating rate, $\mu$, was the only evolving variable. We assume that mating rate has an upper limit at $\mu_{\max }$, determined by physiological and behavioral constraints on the initiation, continuation, and termination of mating events. As often observed in externally fertilizing fishes, the female is assumed to solicit matings by adopting a specific posture, and the male is assumed both to accept these solicitations to the extent allowed by his sperm supply, and to be unable to force matings.

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

Sperm Stocked at Maturation

Analogous to the stock of eggs, a maturing male may have a fixed amount of sperm $\sigma$ available to expend during the entire mating interval of duration $\tau$ (Boivin et al., 2005; Docker et al., 2019; Michalik and Lipke, 2013; Wootton and Smith, 2014). He allocates $S$ sperm per bout, dispensing all available sperm during $\tau$. For males with a single mate, we allow for withholding the fraction $\rho$ from each sperm release to allow for opportunistic mating or for the recruiting of an additional mate (Cornwallis and Birkhead, 2006). This means that
$S_{1}=\frac{(1-\rho) \sigma}{(\mu \tau)}$.

Here, $S_{1}$ has the subscript 1 to indicate that the male has a single mate.

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

We emphasize the contrasting levels of sperm release in $S_{1}$ and $S_{2}$, where the subdivided sperm supply reducing sperm release per mating bout in $S_{2}$ and possible sperm withholding ( $\rho$ > 0 ) in $S_{1}$ determine their relative magnitudes.

## Sperm Recharge

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

See Figure 2B. Following the assumptions that having two mates doubles the male's frequency of mating, and that the male in this case expends all available sperm in each mating bout (i.e. $\beta=$ 0 ), we have
$S_{2}=s(1 /(2 \mu))=s_{\max }\left(1-e^{-\frac{\gamma}{(2 \mu)}}\right)$.

See Figure 2C.

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


Figure 2 Dynamics of continuous sperm recharge. A. Sperm per mating $S=s(1 / \mu)$, where males that mate at frequency $\mu$ can produce sperm between mating bouts over time the time $1 / \mu$. Sperm are produced with diminishing returns as the stock approaches the storage limit $s_{\text {max }}$. The
coefficient $\gamma$ is the rate constant for sperm accumulation. B. Sperm availability over time, when mating with a single female while maintaining the proportion $\rho$ of $s_{\max }$ in reserve at each mating time. C. Sperm availability over time, when a male alternates regular mating with two females, each at frequency $\mu$; his interval between mating bouts is $1 /(2 \mu)$. We assume that no reserves are retained in this case.

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

## Fitness

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

When the male has a single mate, eggs are fertilized at the efficiency $\lambda_{1}$, obtained by substituting $E$ (from equation (2)) and $S_{1}$ (from equation (3) or (5), depending on the mode of sperm production) into equation (1). Incorporating the total number of eggs released $\varepsilon$ and the time interval $\tau$ during which these are released produces an overall single-mate fertilization rate of $\lambda_{1} \varepsilon / \tau$. Similarly, when the male has 2 mates, $S_{2}$ (from equation (4) or (6)) is substituted into equation (1) to obtain $\lambda_{2}$, yielding a 2 -mate fertilization rate of $\lambda_{2} \varepsilon / \tau$. Figure 1 illustrates how the
parameters and key variables link mating to fitness (here, number of offspring successfully produced) for the two different types of sperm production: sperm recharge and a total stock of sperm set at maturation.

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

Moreover, we express any fitness costs per mating, arising for example from physical damage to mates or enhanced predation risk (Daly, 1978; Parker, 1970b; Rowe, 1994) with negative exponential functions of the mating rate $\mu$ and sex-specific coefficients $c_{f}$ and $c_{m}$. Putting these features together, based on the total number of eggs $\varepsilon$ provided by each female, allows us to express male and female fitness $F$ via expected total offspring production over the reproductive interval $\tau$, depending on the number of females attended by the male, as
$F_{f 1}=\theta \varepsilon \lambda_{1} e^{-c_{f} \mu}$,
$F_{m 1}=\theta \varepsilon \lambda_{1} e^{-c_{m} \mu}$,
$F_{f 2}=\varepsilon \lambda_{2} e^{-c_{f} \mu}$, and
$F_{m 2}=2 \varepsilon \lambda_{2} e^{-2 c_{m} \mu}$,
where the subscripts of fitness indicate the relevant sex and the number of females attended by the male.

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

## Solving the Game Between Mates

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

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

Results

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

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

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


Figure 3 Fitness and fertilization efficiency as functions of mating frequency in 3 examples, when sperm are recharged continuously. All parameter magnitudes are as in Table 1 except as specified. Blue lines (b) in left-hand panels are male fitness and red lines (r) indicate female
fitness when the male is mating with a single female. The black line $(\mathrm{k})$ is the male fitness when he is mating with two females; the cyan line (c) shows the female's fitness in that case. Fertilization efficiencies (right-hand panels) are shown for when the male mates a single female (red line, r ) vs 2 females (black line, k ). In panels $\mathbf{A}$ and $\mathbf{B}$, the male fitness multiplier $\theta=2.1$. Both the male and female maximize their fitness with a single mate, which results in consensus monogamy, outcome 1. A Male and female fitness are indicated by the red dashed line, where females maximize their fitness at $\mu^{*}$. B Fertilization efficiencies are maximized near the optimal mating rate. Unsurprisingly, the efficiency is consistently higher for a male with one mate than for a male with two. $\mathbf{C}$. In this case, the male fitness multiplier $\theta=1.2$. The male is always better off with a second female, which is the female's only option. Both fitness curves of the polygynous male (black) and his mate (cyan) are maximized at $\mu^{*}$, corresponding to the vertical cyan line. This pattern is polygyny, outcome 2 . D. As in $\mathbf{B}$, with very similar efficiencies. $\mathbf{E}$. Here, the male fitness multiplier $\theta=1.5$, the default magnitude. The negotiated settlement is a mating frequency just above the black dashed line, indicating where blue and black lines intersect at $\mu^{*}$. The male is restricted to a single mate. This pattern is referred to here as negotiated monogamy, outcome 3. F. Efficiencies are very similar to those in $\mathbf{B}$ and $\mathbf{D}$.

The first outcome, which we refer to as "consensus monogamy", or outcome 1 , corresponds to a situation where the male benefitted from having a single mate at all mating frequencies, involving no conflict between mates over sperm allocation to an additional female. In this situation (Figure 3A), male and female fitness peak near the same mating rate. In this example we assume that females could maximize their fitness instead of the male's; their slightly lower optimal mating rate than that of males resulted from higher mating costs under our
assumed standard parameter magnitudes, and a lower mating rate is easily enforced by slowing down the mating process (see Appendix A), allowing female preference to dominate (red dashed line). Fertilization efficiencies (Figure 3B) are moderately high but higher for the male with a single mate.

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

The third outcome, which we refer to as "negotiated monogamy", or outcome 3 , is depicted in Figure 3E. In this case, the male benefited from having a second mate below a pivotal mating frequency $\mu^{*}$, above which he was better off with a single mate. Because the female's fitness was much lower regardless of mating rate if she shared her mate, she would solicit mating from the male (Briskie, 1992; as often observed; Hatch, 1987; Hatchwell and Davies, 1992) to a level just beyond the frequency at which he benefited from having a single mate. If the male would not mate that frequently, the female had a strong incentive to seek another mate to avoid the severe fitness cost of sharing, providing strong encouragement for the male to go along. Thus, the negotiated mating frequency was just above that at the pivotal
frequency; fitness declined for mates above this cutoff, eliminating any incentive to mate more frequently. Fertilization efficiencies (Figure 3F) were similar to those for the other two outcomes, here based on the higher mating rate at $\mu^{*}$.

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

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

We answer this question by comparing the examples in Figures 3 (sperm recharge) and 4 (stocked sperm). The same three outcomes (Figures 4A, 4C, and 4E) in same sequence with respect to parameter magnitudes are found for stocked sperm as for sperm recharge, following the same logic in accounting for each outcome. Outcome 3 (negotiated monogamy) yields a similar mating rate $\mu^{*}$ (Figure 4E vs 3E) but slightly higher fertilization efficiencies with stocked sperm relative to sperm recharge (Figure 4F vs 3F). A key distinction arises with the other two outcomes. In both outcome 1 (Figure 4A) and outcome 2 (Figure 4C), the optimal mating frequencies are shown as zero, which implies biologically that the highest fitness is achieved
with a single mating over the entire mating interval-in other words, fertilization of the female's entire egg load happens all at once with all of the male's sperm. The single mating bout (i.e. no repeated mating) maximizes fitness in this case because fertilization efficiency is maximized at the minimal mating rate, as a result of higher likelihood of sperm-to-egg contact for a given sperm:egg ratio with more eggs per mating bout. This negative relationship between efficiency and mating frequency results from a fertilization exponent $x<1$, consistent with trend anticipated in the Methods. In contrast, sperm recharge results in a sharp decline in fertilization efficiency as the mating rate becomes very small, because sperm production per mating bout is constrained by the upper limit $S_{\text {max }}$, while egg number per bout increases with a declining mating frequency. This effect ensures that the optimal mating rate for any of the three outcomes is positive, generally implying multiple mating episodes, for sperm recharge.


Figure 4 Fitness and fertilization efficiency as functions of mating frequency in 3 examples, when the stock of sperm is set at maturation. All parameter magnitudes are as in Table 1 except as specified. Blue lines (b) in left-hand panels are male fitness and red lines (r) indicate female fitness when the male is mating with a single female. The black line $(\mathrm{k})$ is the male fitness when
he is mating with two females; the cyan line (c) shows the female's fitness in that case. Fertilization efficiencies (right-hand panels) are shown for when the male mates a single female (red line) vs 2 females (black line). In, panels $\mathbf{A}$ and $\mathbf{B}$, the male fitness multiplier $\theta=2.1$. The male has a single mate. Male and female both maximize their fitness at $\mu^{*}=0$. This pattern is consensus monogamy, outcome 1. B. Fertilization efficiency declines with increasing mating rate, because the fewer eggs per mating are fertilized less efficiently. $\mathbf{C}$ and $\mathbf{D}$. Here, the male fitness multiplier $\theta=1.2$. The male has a single mate.; the male is always better off with a second female, which is the female's only option. Both fitness curves are maximized at $\mu^{*}=0$. This pattern is polygyny, outcome 2. The fertilization efficiencies here are similar to those in $\mathbf{B}$. $\mathbf{E}$ and $\mathbf{F}$. Here, the male fitness multiplier $\theta=1.5$, the default magnitude. The negotiated settlement is a mating frequency just above the black dashed line, indicating where blue and black lines intersect at $\mu^{*}$. The male is restricted to a single mate. This is referred to negotiated monogamy, outcome 3. Fertilization efficiencies are very similar to those in $\mathbf{B}$ and $\mathbf{D}$.

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

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

With the parameter $\theta$, we represent the additional contribution to reproductive success in a nest that a male makes by restricting himself to a single mate, rather than two. Figure 5 shows how the mating rate, outcome, and fitness depend on the magnitude of $\theta$. With $\theta=1$, there is no reproductive advantage per nest of the male's fidelity to one mate regardless of the sperm
production mechanism, and outcome 2 with the male attending two mates is the stable outcome (Figures 5A and 5C). For intermediate magnitudes of $\theta$, the result is outcome 3 (negotiated monogamy), with mating rate steeply declining for larger $\theta$. Magnitudes above about 1.65 (sperm recharge, Figure 5A) or 1.9 (stocked sperm, Figure 5B), the result is outcome 1 (consensus monogamy). Except in the zone of outcome 3, mating frequencies are low and independent of $\theta$ (sperm recharge) or minimal (i.e. once for the female's entire egg load, stocked sperm). Fitnesses are constant within sex and differ in favor of males by about a factor of 2 in the outcome-2 zone, converging to nearly identical magnitudes for the other outcomes, with magnitudes rising from the increased levels of male help. Overall, the magnitude of male help and the extent to which this reproductive contribution can become diluted by a males's divided loyalties between females strongly influences the mating patterns expected to arise.


Figure 5 Mating frequencies and fitnesses over a range of the male fitness multiplier $\theta$. Vertical dashed lines indicate default parameter magnitudes. In the mating frequency panels, red lines (r) are outcome 1 , cyan lines (c) are outcome 2 , and black lines (k) correspond to outcome 3 . In the fitness panels, blue lines (b) are male fitness and red lines (r) are female fitness. A and $\mathbf{B}$, the sperm recharge case. $\mathbf{C}$ and $\mathbf{D}$, stocked sperm.
$\underline{\text { Why might females sometimes withhold eggs during mating bouts? }}$

Consider first the sperm recharge case. With default parameter magnitudes (Table 1), females are better off not withholding eggs (Figure 6A, red line)—their highest fitness
corresponds to $\beta=0$. However, changes in some of the parameter magnitudes yields magnitudes of $\beta$ between 0 and 1 with higher female fitnesses than for $\beta=0$. Figure 6 contains five examples with a range of $\beta$ magnitudes producing increased female fitness. In each case, the relevant range of $\beta$ is between a pair of vertical dashed lines on the figure, with the maximal-fitness magnitude of $\beta$ indicated by a solid vertical line. These are for a total number of eggs per female $\varepsilon=10,000$ (default $\varepsilon=50,000$ ) (Figure 6B); raising either the sperm:egg fertilization coefficient $\phi$ from 0.003 to 0.007 or the maximum sperm recharge $s_{\max }$ from 50,000 to 117,000 (Figure 6C); increasing the sperm production coefficient $\gamma$ from 3 to 7 (Figure 6D); increasing the total reproductive interval duration $\tau$ from 96 hours to 480 hours (Figure 6E); and decreasing the fitness multiplier for male help from 1.5 to 1.3 (Figure 6F).


Figure 6 Fitnesses of males (blue lines) and females (red lines) vs the blank or withheld-fraction of mating bouts $\beta$ when eggs are not released by the female. Males engage in sperm recharge.

Vertical dashed lines bound the magnitudes of $\beta$ where females are able to increase their fitness relative to $\beta=0$ by withholding eggs at those frequencies. Solid vertical lines indicate the fitness
maximizing (optimal magnitude) of $\beta$. A All parameters are at default magnitudes (Table 1), and outcome 3 (negotiated monogamy) prevails over the whole range of $\beta$. In all other cases here, the patterns arise with outcome 2 (polygyny) at $\beta=0$, shifting to outcome 3 at some higher magnitude of $\beta$. B: Total eggs per female $\varepsilon=10,000 . \mathbf{C}$ Either $\phi=0.007$ or $s_{\max }=117,000 . \mathbf{D} \gamma=$ 7. $\mathbf{E} \tau=480 . \mathbf{F} \theta=1.3$.

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

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

## Discussion

In this analysis, we addressed the possibility that repeated within-pair mating could be a way to resolve the sexual conflict over fertilization efficiency and dilutable benefits in external fertilizers. We showed that repeated within-pair mating can be a mate guarding tactic used by females to manipulate males into monogyny through increased fertilization efficiency and increased benefits provided by males to their joint offspring. Despite mating costs that favor low mating frequency for some parameter values, other magnitudes (discussed below) allowed
females to raise mating frequency up to a level that secured monogamy. Under the default parameter values, based on lamprey reproductive biology, the ESS mating frequency reached 10 matings per hour, similar to what is observed in these animals (Applegate, 1950; Malmqvist, 1983; Manion and Hanson, 1980).

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

In place of the classical direct/indirect categorization for male-provided benefits (Andersson, 1994), we used the alternative concept of dilutable benefits proposed by Tazzyman et al. (2012). They emphasized that the distinction between fixed benefits whatever the number of mates and those that are dilutable among the male's mates could shape the form of female preference. Instead of a binary categorization, we modelled benefit dilutability as a continuous feature through the parameter $\theta$, which quantified the benefit to the offspring of a monogamous father relative to the offspring of a polygamous one. This quantitative approach showed that the
dilutability of benefits could affect the evolutionarily stable outcome (monogamy, polygyny, negotiated monogamy) and the mating rate at equilibrium (Figure 5). For example, when a male fish accommodates the eggs of all his mates in a single nest (Jones et al., 2001; Kraak et al., 1999), the size of the nest can set the dilutability of the benefits it provides: egg survival would depend less on the number of females which oviposited in it (i.e. less dilutable benefit) in a large nest than in a small nest. In such a system, our model predicts that negotiated monogamy and repeated mating should be found in nests of intermediate size, while monogamy and polygyny with low mating rate should be observed in small and large nests, respectively.

A central role in our model was played by gamete management from both the male and female perspective. Females of species with marked seasonal reproduction usually start the season with a finite stock of oocytes that may mature all at once or in batches, a feature known as determinate fecundity in fishes (Ganias et al., 2015) and pro-ovigeny in insects (particularly in parasitoids, Jervis et al., 2001). Moreover, females of externally fertilizing species can control the frequency with which they release their eggs to have them fertilized by their mates' sperm during mating (Kiflawi, 2000; Shapiro and Giraldeau, 1996). They can also occasionally withhold eggs despite adopting the usual mating posture that in this case triggers ineffective ejaculation (Jones and Ball, 1954; Esteve, 2007; Schneider, 1971; Ridgway et al., 1989; Roy and Pal, 1986; Yamazaki and Koizumi, 2017; Petersson and Järvi, 2001). This deceptive behavior can be quite frequent, reaching for example $65 \%$ of matings in the Arctic lamprey (Yamazaki and Koizumi, 2017). Outcome 3 (negotiated monogamy), emerging under some magnitudes of our model's parameters, indicates that females may adjust their rate of egg release, and hence the rate of within-pair mating. This can maximize female fitness based on the sperm supplied and the dilutable male-provided benefits. We also showed that under some conditions, withholding eggs
for a substantial proportion of matings could be adaptive for the females because all other parameters being equal, it could result in a shift from polygyny to negotiated monogamy and an associated increase in female fitness. The proportion of eggs withheld having a quite weak effect on female fitness (flat curve around optimum in Figure 6) and a negative effect on male fitness, one could expect males to evolve counteradaptations. However, efficient external fertilization often requires males to ejaculate synchronously or even slightly before egg release, especially under sperm competition (Fitzpatrick and Liley, 2008; Yeates et al., 2007), despite the risk of getting tricked by females. Our model indicates that egg withholding could favor the evolution of mating rate as a male-guarding strategy in females, but the probability of withholding ( $\beta$ ) was not allowed to evolve. On the other hand, we suggest that future attempts to understand the evolution of egg withholding in external fertilizers should account for its possible role as a mate guarding strategy.

The male-female settlement on mating rate obtained under outcome 3 resembles the logic of reproductive skew (e.g. see Buston and Zink, 2009), except that the negotiations here are between sexes rather than within sex. As in transactional models of reproductive skew, where a dominant individual grants just enough reproduction to group members so that they benefit more by staying and helping than by leaving, here the female ensures a mating rate just sufficient to incentivize the male to stay, and to secure exclusive access to dilutable benefits. In transactional models of reproductive skew, the access of subordinates to reproduction is limited to what the dominant consents to give. Yet one subtlety of our model arises from physiological processes such as sperm recharge rate or amount of stored sperm that impose a limit on the staying incentives the male can accept from the female. Sperm management, and in particular the dynamics of spermatogenesis, had major effects on the evolutionarily stable outcome of the
sexual conflict addressed by our model. First, repeated within-pair mating was predicted to some extent under all three outcomes (1: consensus monogamy, 2: polygyny, 3: negotiated monogamy) when sperm was recharged after ejaculation, whereas it was predicted to occur only under negotiated monogamy in the case of finite stock (Figures 3-4). Second, within each scenario of spermatogenesis, parameters pertaining either to the maximum sperm storage, to the reserve held at each ejaculation, or to the rate of sperm production affected the outcome (1,2 or 3 ) and the mating rate (see Appendix B).

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

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

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

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

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

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

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

3: Negotiated monogamy. There is some mating frequency at which $\mathrm{M}-1=\mathrm{M}-2$. In this case, letting the mating rate of equality be $\mu^{*}, \frac{d F_{m 2}}{d \mu}<\frac{d F_{m 1}}{d \mu}$ at $\mu^{*}$, with both slopes negative. The
intersection requires that male fitness is higher with two females than with one at low mating rates because of efficient use of sperm; but fitness is lower with two females than with one at high mating rates because of less efficient sperm use. In this case, females need to avoid sharing their mate with an additional female, because F-2 is generally much lower than F-1. Females seeking to accomplish this may solicit mating. Males will comply because in this situation females will avoid or abandon males with a second female. The compromise reached at $\mathrm{M}-1=$ M-2 can be considered the result of "negotiation". This is an evolutionarily stable outcome, because neither male nor female can increase fitness by imposing a different mating rate.

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

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

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

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

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


Figure B1


Figure B2


Figure B3






Figure B4

