Selection on female remating interval is influenced by male sperm competition strategies and ejaculate characteristics

Suzanne H. Alonzo and Tommaso Pizzari

Female remating rate dictates the level of sperm competition in a population, and extensive research has focused on how sperm competition generates selection on male ejaculate allocation. Yet the way ejaculate allocation strategies in turn generate selection on female remating rates, which ultimately influence levels of sperm competition, has received much less consideration despite increasing evidence that both mating itself and ejaculate traits affect multiple components of female fitness. Here, we develop theory to examine how the effects of mating on female fertility, fecundity and mortality interact to generate selection on female remating rate. When males produce more fertile ejaculates, females are selected to mate less frequently, thus decreasing levels of sperm competition. This could in turn favour decreased male ejaculate allocation, which could subsequently lead to higher female remating. When remating simultaneously increases female fecundity and mortality, females are selected to mate more frequently, thus exacerbating sperm competition and favouring male traits that convey a competitive advantage even when harmful to female survival. While intuitive when considered separately, these predictions demonstrate the potential for complex coevolutionary dynamics between male ejaculate expenditure and female remating rate, and the correlated evolution of multiple male and female reproductive traits affecting mating, fertility and fecundity.

1. Introduction

Parker recognized two major evolutionary implications of female polyandry. First, when females have the opportunity of mating with multiple males, ejaculates can compete over the fertilization of a set of ova, a process known as ‘sperm competition’ [1]. Second, polyandry causes potential for a conflict of fitness interests between the female and her prospective mates with respect to different reproductive decisions, such as the rate at which a female should mate with new males, differential female sperm selection for fertilization, and differential parental investment [2,3]. Here, we focus on conflict over female remating and investigate the consequences of male traits involved in sperm competition for female fitness and selection on female remating behaviour.

Extensive research has focused on understanding sperm competition as a component of sexual selection and an evolutionary agent of traits involved in mating and fertilization [4–6]. This work has shown that in several species the outcome of sperm competition is influenced by male investment in traits, such as the number of viable sperm delivered by an ejaculate [7–12], and/or the rate at which sperm are retained in the fertilizing pool [13–16]. The energetic demands of ejaculate production are sufficiently high that males must trade off ejaculate expenditure with investment in other reproductive traits [4,17,18]. An extensive theoretical framework has been developed to examine the evolution of male strategies of economic ejaculate allocation under varying levels of sperm competition [4,19]. A subset of sex allocation theory [20], ejaculate economic theory, is a powerful tool to understand variation in ejaculate expenditure in the light of sperm competition at multiple levels, from
As far as we are aware, no theory has examined explicitly how female remating rate is expected to respond to effects of mating and male ejaculate allocation on female fitness. Here, we address this gap by presenting new theory to examine selection on female remating rate in response to patterns of male sperm investment and ejaculate characteristics. We first develop a general framework for thinking about the various interacting factors that influence selection on female remating rate. We then consider if and when feedbacks may arise between female remating rate and male adaptations to sperm competition. All else being equal, increased selection on female remating will shorten female remating intervals which will increase the level of sperm competition, while prolonged female remating intervals will relax competition among ejaculates. The evolution of female remating interval therefore has direct consequences for sperm competition, which may drive selection on both male and female traits involved in mating, fertilization and sperm competition. Consequently, it is important to examine how male traits affect selection on female mating patterns as a first step in predicting the coevolutionary dynamics of female and male traits involved in mating, sperm competition and fertilization.

2. A general life-history model of selection on female remating interval

Here, we examine how positive and negative effects of mating and ejaculate characteristics interact to affect selection on female remating rate. We first describe a general life-history model, extended to consider these effects. We then derive a more specific version of this model to make predictions regarding how female survival costs of remating interact with sperm depletion and male effects on female fecundity to determine selection on female remating rate. Both of these formulations (equations (2.1) and (3.1)) make the following assumptions: we assume that reproduction (i.e. mating and offspring production) occurs continuously (rather than seasonally) but that mating and offspring production do not occur simultaneously (i.e. females alternate between mating and producing offspring). In addition, our discrete time life-history model is based on the assumption that each single mating event is followed by one or more offspring-producing bouts (the number of which determines the remating interval). Finally, for simplicity, we assume that females control whether or not they mate, and that females adopt a single remating interval. In other words, we do not consider here the possibility that female remating interval, survival, fecundity or fertility depend on female age or other state variables (but see [49]) or that other female traits or behaviours might evolve with female remating interval. While these possibilities are biologically plausible under some conditions, exploring these effects is beyond the scope of this study. We first focus on how female remating interval affects female fitness, and do not examine selection on, or variation in, other female traits or behaviours.

A female's expected reproductive success in a given time period will depend on the probability she will survive (S) from birth to the current offspring-producing time period, her fecundity in this offspring-producing period (F, the number of eggs produced) and her fertility at this time (P, the probability her eggs will be fertilized; see table 1 for a
Consider a reproductively mature female, and let $m$ represent the number of times she has mated, $\tau$, the number of offspring-producing bouts between mating events and $t$, the number of offspring-producing time periods since the last mating event. We are interested in how variation in $S$, $F$ and $P$ (arising from variation in $t$, $m$ and $\tau$) affect selection on the remating interval ($\tau$). Let $T$ represent the maximum number of offspring-producing bouts or time periods (which could under some conditions be infinite). The expected lifetime reproductive success of a female ($W(\tau)$) is the sum of her expected reproductive success across all time periods (where she first mates and then produces offspring for $\tau$ time periods before mating and producing offspring again). This yields

$$W(\tau) = \sum_{m=1}^{\lceil T/\tau \rceil} \sum_{t=1}^{\tau} S(t, m, \tau)P(t, m, \tau)F(t, m, \tau),$$  

where the notation $\lceil T/\tau \rceil$ indicates a ‘ceiling function’ which rounds up to the next integer. If the maximum number of offspring-producing bouts ($T$) is not an integer multiple of the number of offspring-producing bouts between matings ($\tau$), the summation will include term(s) for after the end of the maximum lifespan where those terms will have the value of zero. This is simply a life-history model of female fitness extended to examine the fitness effects of female remating interval ($\tau$) and consider the effects of fecundity ($F$) and fertility ($P$) on reproductive success separately (given the assumptions outlined above). The relative fitness of a particular remating interval will depend on how mating affects survival, fertility and fecundity. In general, we would expect female fertility (i.e. the probability of fertilization) to decline with time since mating. The rate of decline will depend on a number of biological factors, such as the number and quality of sperm received from the male as well as patterns of female sperm storage and usage. While fertility will usually decline as remating rate decreases, remating rate and the time since last mating can have both positive and negative effects on female survival and fecundity [50]. Selection on female remating interval will therefore depend on the complex balance between these multiple positive and negative effects of mating.

3. A more specific example of selection on female remating interval

The equation (2.1) is neither intended nor able to yield specific predictions. Instead, it captures the multiple effects that mating may have on female fitness. In order to make more quantitative predictions, we need to make specific assumptions about how survival, fertility and fecundity are affected by male ejaculate characteristics and female remating rate. Consider the following biological scenario: imagine that each mating event carries an immediate additional risk of mortality ($\mu$), where $1 - \mu$ gives the probability of surviving each mating (which is assumed here to be static rather than a function of time since mating or the number of mating events). Let $s$ represents the baseline probability of surviving between offspring-producing periods, independent of mating (assumed to be static as well). We will assume as above that

### Table 1. Definitions for key variables and parameters used in the model.

<table>
<thead>
<tr>
<th>Description</th>
<th>Variable</th>
<th>Formula</th>
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<tbody>
<tr>
<td>female lifetime expected fitness</td>
<td>$W(\tau)$</td>
<td>---------</td>
</tr>
<tr>
<td>number of offspring-producing bouts since the last mating</td>
<td>$t$</td>
<td>---------</td>
</tr>
<tr>
<td>number of mating events</td>
<td>$m$</td>
<td>---------</td>
</tr>
<tr>
<td>remating interval (the number of offspring-producing bouts between mating events)</td>
<td>$\tau$</td>
<td>---------</td>
</tr>
<tr>
<td>maximum number of offspring-producing bouts (can be infinite)</td>
<td>$T$</td>
<td>---------</td>
</tr>
<tr>
<td>probability of survival from birth to time period $m\tau + t$</td>
<td>$S(m, \tau)$</td>
<td>---------</td>
</tr>
<tr>
<td>probability of survival between offspring-producing bouts</td>
<td>$s$</td>
<td>---------</td>
</tr>
<tr>
<td>survival cost per mating, $1 - \mu$ is the probability of surviving each mating event</td>
<td>$\mu$</td>
<td>---------</td>
</tr>
<tr>
<td>quantity of viable sperm stored by a female at time $t$ since the last mating $m$</td>
<td>$N(t, m, \tau)$</td>
<td>---------</td>
</tr>
<tr>
<td>probability of fertilization $t$ periods since the last mating</td>
<td>$P(t, m, \tau)$</td>
<td>---------</td>
</tr>
<tr>
<td>quantity of viable sperm received from a male at each mating</td>
<td>$n$</td>
<td>---------</td>
</tr>
<tr>
<td>proportion of stored sperm remaining after each new mating event</td>
<td>$p$</td>
<td>---------</td>
</tr>
<tr>
<td>the proportion of sperm lost or depleted between offspring-producing periods</td>
<td>$d$</td>
<td>---------</td>
</tr>
<tr>
<td>fertilization rate</td>
<td>$f(t, m, \tau)$</td>
<td>---------</td>
</tr>
<tr>
<td>female fecundity</td>
<td>$f$</td>
<td>---------</td>
</tr>
<tr>
<td>baseline female fecundity (without male effect)</td>
<td>$f_0$</td>
<td>---------</td>
</tr>
<tr>
<td>maximum effect of mating on female fecundity</td>
<td>$f$</td>
<td>---------</td>
</tr>
<tr>
<td>proportion of $\phi$ remaining following each time period since last mating</td>
<td>$\rho$</td>
<td>---------</td>
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</table>
females produce offspring in discrete reproductive bouts (or time periods) and that they may mate between these bouts, where $\tau$ represents the number of offspring-producing bouts between mating events (figure 1).

Female expected lifetime reproductive success then becomes

$$W(\tau) = \sum_{m=1}^{[T/\tau]} (1 - \mu)^m \sum_{t=0}^{\tau} \binom{m-1}{t-1} P(t, m, \tau) F(t, m, \tau),$$

(3.1)

where, as in equation (2.1), the notation $[T/\tau]$ indicates a ‘ceiling function’ which rounds up to the next integer. If the maximum number of offspring-producing bouts ($T$) is not an integer multiple of the number of offspring-producing bouts between matings ($\tau$), the summation will include terms after the end of the maximum lifespan which will have the value of zero. From this equation, one can see that (as in the more general case presented above) the optimal remating interval will be determined by a balance between the negative effect of mating on survival (e.g. $\mu$), the positive effects of mating on fertility (e.g. changes in $P$ with $t$) and the way in which male traits and remating rate affect female fecundity (e.g. how $F$ changes with $t$, $m$ and $\tau$). Next, we derive specific equations that capture how female fecundity and fertility are affected by remating rate and male ejaculate traits, under the assumption that mating itself is costly (as represented in equation (3.1)).

(a) Sperm storage and depletion

We assume that the amount of viable sperm available to a female declines between mating events due to sperm depletion (e.g. the rate at which sperm become unavailable or inviable over time). The dynamics of sperm storage (and use) between mating events will also influence the total amount of viable sperm available to a female.

Here, we consider the scenario where female sperm storage capacity does not limit the maximum quantity of viable sperm available for fertilization and where a proportion ($p$) of the remaining sperm from each earlier ejaculation is removed at each new mating (where $0 < p < 1$). Here, the total amount of viable sperm stored is determined by the number of new sperm delivered by the current insemination ($n$), the proportion of sperm lost or depleted between time periods ($d$) and the proportion of viable sperm remaining from earlier matings ($p$, figure 2a). Females therefore ‘accumulate’ sperm as they mate with multiple males over their lifetime. Let $N(t,m,\tau)$ represent the number of viable sperm stored by a female that has survived $m$ mating events, with $\tau$ reproductive bouts between each mating and whose last mating occurred $t$ time units ago where

$$N(t, m, \tau) = n(1 - d)^t + np(1 - d)^{(t+1)} + \cdots + np^{(m-1)}(1 - d)^{(m-1)+t}$$

$$= \sum_{i=1}^{m} np^{(i-1)}(1 - d)^{(i-1)+t}.$$  

(3.2)

Over time, there will be a balance between the input of new viable sperm (determined by $n$ and $\tau$) and the loss of viable sperm (determined by $p$ and $d$, figure 2a). Note that this equation assumes that sperm begin to decline in viability and availability immediately after mating (such that $N(1,1,\tau) = n(1 - d)$ rather than $n$). This is consistent with the idea that females store sperm and a delay exists between mating and the first bout of fertilization and offspring production. For species for which this is not a reasonable assumption, $t$ would be replaced with $t - 1$ in equation (3.2). This has little quantitative and no qualitative effect on the outcome of the model.

While this sperm storage scenario represents only one option of multiple biologically plausible scenarios, it allows for the entire continuum between no storage ($p = 0$) and complete storage ($p = 1$), and therefore captures a broad range of dynamics and species. All else being equal, females will be more sperm limited as $p$ decreases (figure 2a,b). It is worth noting that remating by a female always decreases the expected share of paternity of her previous mates, as long as some of their sperm remain viable. Therefore, conflict between the sexes with respect to paternity and female remating always exists at some level as long as the sperm of a male has nonzero probability of fertilization if the female does not mate again with another male. Our analyses focus on how the effects of mating on female fecundity, fertility and survival interact to shape selection on female remating interval.

(b) Female fertility

The probability of an egg being fertilized is typically an asymptotically increasing function of the number of viable
that total time proportion depleted per time period (retained (probability of fertilization time (limit of equation (3.2) for Figure 2. P(3.2)) and can be represented by the general equation [7,11,12]. The probability of fertilization (r viable sperm stored by the female (a) The number of viable sperm available to a female varies over time (and here time is determined by the time since last mating (t), number of mating events (m), the remating interval (τ), such that total time = τm + t), the number received at each mating (n), the proportion depleted per time period (d), and the proportion that remain after each new mating event (p). (a–c) Black lines represent p = 0.01, dashed lines p = 0.5 and grey lines p = 1, and results shown are for d = 0.1, n = 100 and τ = 5. (b) Females that have mated multiple times reach an asymptotic maximum level of sperm storage which depends on remating interval (τ), proportion of sperm retained (p) and sperm depletion (d), mathematically this is given by finding the limit of equation (3.2) for t = 0 as m→∞ or n/(1 − p(1 − d)−1). (c) The probability of fertilization P(t,m,τ) varies with the number of available sperm and fertilization rate (shown here for N(t,m,τ) from (a) and τ = 0.01).

given in equation (3.2) (figure 2c). In equation (3.3), e−rN(t,m,τ) represents the probability that all of the available viable sperm will fail to fertilize the egg (i.e. the probability no fertilization occurs based on a Poisson distribution where the mean number of ‘events’ is λ = rN(t,m,τ)). The parameter r represents the relative number of sperm required for fertilization and will vary among species depending, for example, on mode of fertilization [30]. Equation (3.3) implies generally that (all else being equal) the probability that an egg will be fertilized declines with time since mating (t), and the rate of decline is determined by the relative value of parameters r, d and n, which determine the amount of sperm needed for fertilization, the rate of sperm depletion following insemination, and the total amount of viable sperm a female obtains at each mating, respectively (figures 2c and 3a). Our analyses focus on how the number of viable sperm received at each mating and the rate of sperm depletion (represented by p and d, respectively), are predicted to affect selection on female remating interval.

(c) Female fecundity

We consider the possibility that mating and/or ejaculate traits can have gonadotropic effects on female fecundity (see §2). Here, we consider the situation where mating has an acute effect on average female fecundity, such that expected fecundity (F(t)) depends on time since last mating (t). This captures the biological case where female fecundity is increased by mating, for example, owing to resources obtained from the male at mating. Let f represents the baseline fecundity of the female without any male effect, ϕ, the maximum effect of mating on female fecundity (which could be positive or negative as long as −f < ϕ) and p gives the proportion of that effect on fecundity that is lost per time period since mating. Female fecundity F(t) can then range between f and f + ϕ depending on time since last mating (t), such that

\[ F(t) = f + \phi t^{-1}. \]

We focus on cases where there is either no effect of mating on fecundity (ϕ = 0) or a positive effect of mating on fecundity (ϕ > 0; figure 3b). In general, we ask how large the positive effect on fecundity must be to outweigh the negative effects of mating on female survival. This allows us to determine the degree to which male traits that affect female fecundity have secondary effects on female mating behaviour (i.e. propensity to remate) and thus sperm competition (figure 3c). We also ask how these costs and benefits of mating interact with male ejaculate characteristics such as the number of viable sperm delivered and the rate of sperm depletion to determine selection on female remating rate. In the future, this framework would also enable one to consider alternative scenarios where fecundity might vary with the number of matings (m), time since reproductive maturity (mt + 1) or remating interval (τ) directly.

4. Results of the specific model

It is not possible to solve the above equations analytically. It is, however, possible to calculate female fitness and find the remating interval (τ) that maximizes female reproductive success for any given set of parameters. We present the results of these numerical analyses both graphically and verbally.
delivered by an ejaculate and the rate of sperm depletion from the female sperm stores, (ii) male/ejaculate effects on female fecundity, and (iii) the interactive effects of female sperm depletion and male/ejaculate fecundity effects.

(a) Female responses to the number of viable sperm and sperm depletion

For simplicity, we first examine the effect of sperm viability and costs of mating in isolation. Consider the situation where mating has no direct effect on female fecundity (i.e. $F = f$ and $\phi = 0$), but carries a risk of mortality for females ($\mu > 0$). Selection on remating interval will then be determined by the joint effect of mating mortality costs ($\mu$) and sperm limitation (represented by the initial number of sperm inseminated ($n$) and the rate of sperm depletion following mating ($d$)) on female fitness. In this case, the only benefit of mating is in avoiding sperm depletion. All else being equal, the optimal remating interval is predicted to increase as the survival cost of mating ($\mu$) increases (figure 4). For a given value of $\mu$, decreasing the amount of sperm a female receives per mating also selects for more frequent mating (figure 4, compare panels from left to right), as does more rapid sperm depletion (figure 4, compare within each panel from bottom to top). The pattern of sperm storage (figure 4, compare across rows) has very little quantitative effect when sperm numbers and quality are relatively high. When sperm limitation is high (e.g. low $n$ or $r$ and high $d$), however, greater sperm storage ($p$ large) is predicted to favour shorter remating intervals (figure 4, far left column). One might expect lower storage to favour shorter intervals, all else being equal, since lower storage reduces the amount of sperm available (figure 2b). Our analyses indicate that the survival cost of mating is only outweighed by the fertility benefits of mating when sperm storage (and the associated potential for high fertility) is high. Perhaps surprisingly, greater sperm storage by females can therefore favour shorter remating intervals, particularly in species where sperm is limiting. It is important to note that even if females achieve their optimal remating interval, they are predicted to tolerate striking reductions in fertility when mating comes at a cost to female survival (e.g. for the optimal remating rate of $\tau = 9$ given by the black line in figure 3c, the associated female’s expected fertility rate is predicted to drop from 100 per cent to approximately 50 per cent before she will mate again, as shown in figure 3a by the solid black line).

(b) Female responses to effects of remating interval on fecundity

We now consider how the effect of mating on female fecundity influences selection on female remating interval. In all of the cases discussed below, we assume that female mortality rate increases with shorter remating intervals (i.e. mating is costly to females, $\mu > 0$) and the probability of fertilization ($P$) decreases over the remating interval (i.e. $d > 0$). When mating increases female fecundity, remating intervals are predicted to be shorter than in the absence of a fecundity effect (figure 5). Thus, while male stimulation of female fecundity may be selected for in males, it may also increase sperm competition as it favours more frequent mating by females. As the magnitude of the fecundity effect increases (i.e. $\phi$ increases relative to $f$), the predicted effect on female remating interval increases as well, with greater fecundity effects selecting for

![Figure 3. Female fertility, fecundity and fitness as a function of remating interval. (a) The probability of fertilization declines with time since last mating. The rate of decline is determined by the total amount of sperm received per mating ($n$) and the proportion of sperm ($d$) that are depleted or become inviable between each offspring-producing period (black line $n = 1000$, $d = 0.25$; grey line $n = 100$, $d = 0.5$). Solid lines represent limited storage ($p = 0.01$), while dashed lines represent nearly unlimited storage ($p = 0.99$) (b) Female fecundity may be unaffected (black line, $\phi = 0$) or increase with mating (grey line $\phi = 1$, $p = 0.25$). (c) Female lifetime expected reproductive success is determined by fertilization, mortality and fecundity (for both lines $f = 1$, $r = 0.01$, $T = 1000$ and $s = 0.99$, other parameters as given for (a) and (b)). Although low and high levels of sperm storage scenarios are shown (dashed and solids lines as in (a)), they mostly overlap for cases with moderate to low sperm limitation and thus have little effect on female expected fitness.](http://rstb.royalsocietypublishing.org/Downloaded from rsta.royalsocietypublishing.org Phil Trans R Soc B 368: 20120044)
shorter remating intervals. Similarly, when the fecundity effects attenuate rapidly ($r$ large), shorter remating intervals are favoured, all else being equal. Examination of the duration of the fecundity ($r$) effect reveals an interaction between the cost of mating and effects of mating on female fecundity: for low costs of mating ($m$ small), the predicted optimal female remating interval is shorter when the fecundity effect is short-lived ($r$ small, figure 5 dashed lines) than when it is long-lasting ($r$ large, figure 5 solid lines). This pattern is reversed, however, at higher costs of mating, with long-lasting fecundity effects favouring shorter remating intervals than short-lived fecundity effects (figure 5, thin solid lines). All else being equal, positive effects of mating favour shorter remating intervals. The magnitude of this effect, however, depends on an interaction between the cost of mating and the duration of the influence of mating on fecundity. Fecundity effects are predicted to have the largest relative effect on remating intervals when sperm limitation is low.

(c) Male per ejaculate allocation effects on female remating interval

The optimal female remating interval depends on an interaction between the number of sperm received per mating ($n$), the rate of decline in fertility ($d$), the effect of remating interval on female fecundity ($f$ and $r$), and the mortality cost of mating ($\mu$), which will depend on the total and relative per ejaculate allocation by males. While both increased allocation to sperm quality (in terms of duration of viability $d$) and quantity ($n$) are expected to select for longer female remating intervals, it is likely that a trade-off exists between these ejaculate traits, such that increases in quantity may...
trade off with quality and vice versa for a given per ejaculate allocation. Similarly, while increased allocation to fecundity effects will favour shorter female remating intervals, all else being equal, increased allocation to traits that affect the cost of mating will favour longer female remating intervals. Thus, while the effect of each male ejaculate trait is relatively intuitive in isolation, the expected coevolutionary dynamics between multiple male ejaculate traits and female remating interval is less clear. At present, it is impossible to predict these dynamics without greater knowledge of how multiple male ejaculates evolve simultaneously in response to female remating rate and how evolutionary ‘tugs of war’ between multiple male and female traits are resolved.

5. Discussion

The realization that strong selection may exist on both males and females with respect to mating frequency has catalysed theoretical interest in the coevolutionary dynamics of remating [3,22,25,47,49,51–53]. When the direction of selection on mating differs between males and females, an evolutionary conflict over mating decisions arises between the sexes, which may influence both male and female behaviour and reproductive traits [3,44]. Unfortunately, the field remains strongly polarized. On the one hand, coevolutionary models that explore sexual conflict over remating often ignore dynamics of male ejaculate allocation underpinning selection on female remating. On the other hand, models of ejaculate economics often ignore the dynamic inter-dependence between male ejaculate allocation and female remating behaviour, and either assume fixed remating rates [54] or assume that remating rates change exclusively owing to selection on males [55,56]. The objective of this paper was to provide a theoretical framework for understanding how fitness effects associated with mating and multiple ejaculate traits simultaneously shape selection on female remating intervals.

Our results illustrate how selection on female remating intervals changes in response to the complex ways in which mating and ejaculate traits interact to affect multiple components of female fitness. We show that, in general, greater female survival costs associated with mating select for longer remating intervals (and thus lower remating rates) in females. However, the magnitude and direction of selection depends on an interaction between fertilization dynamics due to sperm depletion rates, the number of viable sperm received by a female and the effect of mating on female fecundity and survival. If changes in female mating behaviour select for changes in male ejaculate characteristics, complex feedback dynamics may result. Predicting these coevolutionary dynamics will require greater knowledge of how female remating affects the correlated evolution of multiple male ejaculate traits.

For example, if males respond to sperm competition by investing preferentially in sperm numbers at the expense of sperm longevity [57,58], the net effect on female mating interval will depend on the relative change in these two traits, as increased sperm number favours longer remating intervals while decreased longevity favours shorter intervals (figure 4). In contrast, if higher levels of sperm competition select instead for greater total investment in ejaculates, then high remating rates may favour increased sperm quantity and quality [59], which then further selects for longer remating intervals (and may subsequently lead to selection on males for decreased allocation to ejaculates). Whether these dynamics lead to stable intermediate remating rates and ejaculate allocation or an unstable arms race will depend on the degree to which males and females determine remating interval (‘power of winning’ [3]) as well as how selection shapes evolutionary male responses to sperm competition and the underlying genetics of traits affecting mating, fertilization and fecundity [60].

We have predicted how female remating interval is expected to evolve in response to male ejaculate characteristics. Other female traits—related to sperm storage, fertilization efficiency and egg production—likely also experience selection arising from male ejaculate characteristics. The evolution of female remating will therefore also depend on the magnitude of selection on and rate of evolution of these related female traits. Further theory and empirical data on the genetic
covariances among multiple male and female traits will be needed to predict the correlated evolution of the many male and female traits involved in mating and fertilization.

Another way to think about the combined effects of mating on female fitness is to ask whether a positive or negative relationship between reproductive output (fertility times fecundity) and survival as a function of remating interval exists. This is somewhat similar to asking whether an interaction is parasitic, mutualistic or altruistic [61, 62]. When all effects are negative (e.g. fertility, fecundity and female survival all decrease with increased remating rate) then selection will clearly favour decreased female remating rates and conflict between the sexes with respect to remating rate will be likely to arise. When a combination of positive and negative effects exists, then individual costs of mating may be evident even if evolutionary conflict (e.g. differences in the direction of selection with respect to female remating, [63]) over mating is not. Further empirical data on the covariance between specific male traits and individual aspects of female fitness (e.g. survival, fecundity and fertility) may yield important insights into net selection on female remating rate and the feedback between female remating rate and selection on specific male traits involved in sperm competition.

Traditionally, strategies of male ejaculate expenditure have been considered assuming fixed levels of sperm competition. More recently, a few studies have considered ejaculate expenditure strategies evolving dynamically with male effects. For example, Parker & Ball [64] proposed a population model in which the level of sperm competition was proportional to the number of matings a male achieves, so that the costs of gaining a mating and male ejaculate expenditure are inter-related. Consistent with traditional ejaculate economic theory (equation (3.3)), the model by Parker & Ball [64] predicts higher ejaculate expenditure with increasing risk of sperm competition in a population. However, in another ‘consistent’ model in which number of mating dictates ejaculate expenditure, Williams et al. [55] argue that higher sperm allocation will necessarily lead males to mate less frequently, thus resulting in lower levels of sperm competition. A recent theoretical study by Fromhage et al. [65] demonstrated that these divergent predictions can be reconciled by considering female mating behaviour, and showed that when females are able to resist mating beyond an arbitrary threshold, mating frequency in the population can become decoupled from patterns of male sperm allocation justifying predictions by Parker & Ball [64]. However, when males are able to impose mating on females, mating frequency becomes intimately linked with male sperm allocation leading to the scenario predicted by Williams et al. [55]. Predictions regarding male and female coevolution may therefore depend on specific biological details of how mating, fertilization and fecundity arise.

We show that selection on female remating interval, determined by multiple fitness effects associated with mating, represents an alternative and intuitive—but so far neglected—evolutionary pathway to both reductions and increases in the level of sperm competition of a population. Two key points emerge from these results.

First, it is important to interpret empirical evidence for antagonistic male ‘manipulation’ of females and sexual conflict over mating due to decreased survival cautiously as only under a net lifetime fitness cost will conflict over remating interval truly exist. For example, if mating increases fecundity or sperm depletion occurs quickly, females may be selected to mate as often as possible and experience low survival. We also find that females may experience large apparent costs of mating even at the predicted optimal remating interval for females. Therefore, costs of mating alone do not necessarily indicate that females are in conflict with males over remating interval, and female remating in the presence of mating costs to female survival is not necessarily indicative of males ‘winning’ the battle over remating rate (note that the absence of sexual conflict over remating rates does not eliminate potential for conflict over female sperm utilization and other reproductive decisions). These predictions are consistent with a recent meta-analysis showing that females often experience net positive fitness effects of multiple mating, selecting for more frequent mating in many species [27].

Second, the results of our study influence our understanding of mating systems evolution. Spatio-temporal variation in female availability has been traditionally explained in terms of patterns of distribution of reproductive resources and female potential reproductive rates [66]. However, our results show that variation in remating rates may also emerge as an intrinsic property of sexual selection on male mating traits that also influence female fecundity and survival. These dynamics are further influenced by species-specific aspects of reproductive physiology, ecology and evolutionary history that, in the context of our model, can generate predictable variation among species and populations with respect to patterns of mating. Therefore, the evolution of mating systems and selection on female remating rate will interact to determine patterns of female availability and male reproduction in ways not captured by existing theory on the evolution of mating systems.

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