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Coevolutionary Feedbacks between Female Mating Interval and Male Allocation to Competing Sperm Traits Can Drive Evolution of Costly Polyandry

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ABSTRACT: Complex coevolutionary feedbacks between female mating interval and male sperm traits have been hypothesized to explain the evolution and persistence of costly polyandry. Such feedbacks could potentially arise because polyandry creates sperm competition and consequent selection on male allocation to sperm traits, while the emerging sperm traits could create female sperm limitation and, hence, impose selection for increased polyandry. However, the hypothesis that costly polyandry could coevolve with male sperm dynamics has not been tested. We built a genetically explicit individual-based model to simulate simultaneous evolution of female mating interval and male allocation to sperm number versus longevity, where these two sperm traits trade off. We show that evolution of competing sperm traits under polyandry can indeed cause female sperm limitation and, hence, promote further evolution and persistence of costly polyandry, particularly when sperm are costly relative to the degree of female sperm limitation. These feedbacks were stronger, and greater polyandry evolved, when postcopulatory competition for paternity followed a loaded rather than fair raffle and when sperm traits had realistically low heritability. We therefore demonstrate that the evolution of allocation to sperm traits driven by sperm competition can prevent males from overcoming female sperm limitation, thereby driving ongoing evolution of costly polyandry.

Keywords: polyandry, ejaculate economics, sperm competition, trade-offs, female sperm limitation, fertility assurance.

Introduction

The evolution of polyandry, defined as female mating with multiple males within a single reproductive event, has far-reaching evolutionary and ecological consequences (Holman and Kokko 2013; Kvarnemo and Simmons 2013; Pizzari and Wedell 2013) yet remains an evolutionary puzzle (Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Simmons 2005; Evans and Simmons 2008; Parker and Birkhead 2013; Forstmeier et al. 2014). Explaining the evolution and persistence of polyandry is particularly challenging when there appears to be negative rather than positive direct selection on multiple mating (i.e., polyandry is costly; Rowe 1994; Chapman et al. 2003; Wigby and Chapman 2005; Sardell et al. 2012; Slatyer et al. 2012). One emerging hypothesis is that polyandry coevolves with male traits. Specifically, evolution of costly polyandry could be driven by complex (co)evolutionary feedbacks between male allocation to ejaculate traits and female multiple mating (Engqvist 2012; Alonzo and Pizzari 2013; Abe and Kamimura 2015). It is well established that sperm competition and consequent dynamics of allocation to ejaculate traits are direct consequences of polyandry (Parker and Pizzari 2010). However, the degree to which such male allocations might, in turn, exert selection on female multiple mating has received less attention (Alonzo and Pizzari 2010, 2013).

The degree of polyandry directly determines the risk and intensity of postcopulatory male competition over fertilization (Parker 1998), thereby exerting strong selection on ejaculate characteristics that increase fertilization success (Calhim et al. 2007; Mossman et al. 2009; Pizzari and Parker 2009; Firman and Simmons 2011; Rowe and Pruett-Jones 2011). The recognition that sperm production can be costly for males (Dewsbury 1982; Nakatsuru and Kramer 1982; Van Voorhies 1992; Olsson et al. 1997; Pitnick et al. 2009) has sparked substantial theory on male resource allocation to pre- and postcopulatory traits under varying levels of polyandry (reviewed in Parker and Pizzari 2010). Such theory and empirical evidence show that the outcome of sperm competition is mainly influenced by two traits: relative sperm number and ejaculate quality (Cook and Wedell 1996; Gage and Morrow 2003; Pizzari and Parker 2009; Parker and Pizzari 2010). "Quality" broadly refers to ejaculate fertilization efficiency after controlling for sperm number and can comprise numerous traits such as sperm lon-

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gevity, size, morphology, velocity, metabolic performance, and seminal fluid composition (e.g., Chapman 2001; Smith and Ryan 2010; Perry et al. 2013; Fitzpatrick and Lüpold 2014). Sperm longevity is particularly important in internally fertilizing species where females can store sperm prior to fertilization (Pizzari and Parker 2009); higher sperm longevity enables males to participate in sperm competition for longer after mating. Indeed, the number of sperm cells that are viable at the moment of fertilization is strongly correlated with a male's fertilization success (e.g., Bernasconi et al. 2002; Hunter and Birkhead 2002; Snook and Hosken 2004; García-González and Simmons 2005; Reinhardt 2007; Pizzari et al. 2008*a*, 2008*b*). Although males' fitness could be increased by high sperm number or quality, investments in such different sperm traits are likely to trade off against each other (Moore et al. 2004; Snook 2005; Helfenstein et al. 2008; Evans 2011; Immler et al. 2011), thereby constraining ejaculate allocation dynamics in multitrait space.

Sperm competition and consequent male allocation to ejaculate traits can also affect female fitness and exert positive and/or negative selection on female multiple mating (South and Lewis 2011; Alonzo and Pizzari 2013). For example, evidence from both internally and externally fertilizing species shows that female sperm limitation, where mated females receive fewer viable sperm than required to fertilize eggs, can reduce female fertility (Levitan and Petersen 1995; Warner et al. 1995; Ball and Parker 2000; Kraus et al. 2004). Female sperm limitation can be exacerbated by male ejaculate allocation strategies (Wedell et al. 2002), male sperm depletion due to multiple mating (Jones 2001; Preston et al. 2001; Harris and Moore 2005; Boivin 2013), and male infertility (Hasson and Stone 2009). Coevolutionary feedbacks between male allocation to ejaculate traits (which may create female sperm limitation) and female mating rate might, therefore, arise, thereby allowing females to adaptively overcome sperm limitation.

Alonzo and Pizzari (2013) proposed a modeling framework that considers the effects of male allocation to ejaculate traits on female fitness and remating interval (i.e., polyandry). They found that when males deliver less sperm, sperm depletion from females' sperm storage is faster and that when remating increases female fecundity, then polyandry increases. Alonzo and Pizzari (2013) hypothesized that changes in female multiple mating could, in turn, cause changes in allocation to ejaculate traits, establishing coevolutionary feedbacks. However, their model did not allow male strategies to evolve, meaning that the hypothesized coevolutionary feedbacks were not evaluated.

Similar feedbacks were hypothesized by Engqvist (2012), who modeled the evolution of male allocation to sperm traits under fixed female remating intervals. Using a game theoretic approach, he investigated the evolution of male allocation to sperm longevity, when longevity and sperm number trade off. Engqvist (2012) found that under decreasing female remating interval (i.e., increasing polyandry and sperm competition), sperm longevity decreased (i.e., sperm became less viable). He hypothesized that when females are sperm limited, such dynamics could cause ongoing evolution of female remating interval and, hence, polyandry. Specifically, if females are sperm limited, there should be initial selection for female remating. The increase in female remating rate would increase sperm competition, possibly leading to lower sperm viability and thereby maintaining sperm limitation, generating a feedback loop that could maintain polyandry.

Despite the potential importance of coevolutionary feedbacks between polyandry and male allocation to ejaculate traits (Parker and Pizzari 2010; Alonzo and Pizzari 2013), very little modeling has explicitly considered these processes or their consequences for the evolution of polyandry. Models that consider both male and female strategies typically do not do so dynamically (but see Alonzo and Pizzari 2010; Abe and Kamimura 2015); either evolution of male ejaculate allocation is considered under fixed levels of polyandry (e.g., Parker and Ball 2005; Williams et al. 2005; Fromhage et al. 2008; Engqvist 2012; Requena and Alonzo 2014) or evolution of polyandry is considered under fixed male strategies (e.g., Hasson and Stone 2009; Alonzo and Pizzari 2013). Abe and Kamimura (2015) presented a game theoretic model where male investment in sperm number and female mating frequency both evolved under sperm limitation caused by an uneven sex ratio. They assumed males had a fixed amount of resources available to partition between mate acquisition and sperm number allocated to each ejaculate. They show a first example of coevolutionary feedback between female and male strategies: under moderately female-biased sex ratios, males evolve to allocate less sperm per ejaculate and females evolve higher mating frequencies to obtain sufficient sperm for fertilization.

However, Abe and Kamimura (2015) did not consider male allocation to different sperm traits or examine whether sperm viability might decrease due to increased female multiple mating. Consequently, we still do not know whether the hypothesized feedbacks with male allocation to competing sperm traits (Engqvist 2012) can drive ongoing evolution of costly polyandry. Here, we present a model that explicitly examines (co)evolution of female mating interval (i.e., polyandry) and male allocation to sperm traits (number and longevity), thus explicitly accounting for emerging evolutionary feedbacks between the two sexes' strategies. We build a genetically explicit individual-based model (IBM) to test the hypothesis that costly polyandry can evolve and be maintained because the resulting sperm competition decreases sperm longevity and, hence, causes female sperm limitation (Engqvist 2012).

We first verify that our basic model reproduces Engqvist's (2012) results regarding evolution of sperm longevity given fixed polyandry. We then allow female mating interval to evolve and test whether the dynamics of male allocation to sperm traits can cause evolution of costly polyandry in the absence or presence of female sperm limitation. We thereby test whether sperm dynamics can maintain female sperm limitation, creating selection for polyandry. We then test whether the form of sperm competition (i.e., the type of lottery that determines paternity) influences these feedback dynamics. Finally, since the strength of coevolutionary dynamics might depend on the relative genetic versus environmental contributions to trait variation, we test whether costly polyandry can still be maintained by feedbacks with sperm dynamics when key sperm phenotypes show substantial environmental variance.

Methods

We simulated a single, freely mixing population with nonoverlapping generations and 1∶1 primary sex ratio. Each generation consists of reproduction (mating, fertilization, and birth) and density-dependent offspring survival. Females mate with a random male at each mating. Hence, female remating within a single reproductive event typically leads to polyandry as there are no constraints for females to remate with the same male (e.g., due to social monogamy; Alonzo and Pizzari 2013).

Genetic Architecture

We considered one female trait, mating interval (τ), and two male traits, sperm number (s) and sperm mortality rate (μ), where $1/\mu$ corresponds to expected sperm longevity. We assumed a diploid autosomal additive genetic system with sex-limited phenotypic expression. Each trait is determined by L physically unlinked loci with no pleiotropy. We assumed a continuum-of-alleles model (Kimura 1965; Lande 1976; Reeve 2000) whereby each allele's initial value is sampled from continuous (normal) distributions. Each individual's genotypic value for each trait (hereafter, g_τ, g_s, and g_μ) equals the sum of its $2L$ allelic values. While g_τ, g_s, and g_μ can take any real value, we constrained phenotypic values to $0.01 \le \tau \le 1$ and $s \ge 1$ and μ to $\ge 10^{-10}$, thereby limiting the maximum number of female matings per egg to 100, precluding males from producing less than 1 sperm cell and avoiding numerical errors due to $\mu = 0$. Offspring inherit a single random allele from each parent at each locus.

We initially assumed no environmental variance; hence, the phenotypic traits τ, s, and μ have heritability $h^2 = 1$. We subsequently relaxed this assumption for s and μ. In this case, to determine a male's phenotype, a random normal deviate with mean zero and standard deviation such that the environmental variance is a proportion ε of the initial genotypic variance is added to g_s and g_μ. The environmental covariance between s and μ is assumed to be zero.

Each allele has a mutation probability per generation of M. When an allele mutates, a random normal deviate with mean m and standard deviation σ_m is added to the allele value (Kimura 1965; Lande 1976). We assumed $L = 20$ for each evolving trait, $M = 0.001$/allele/generation, $m = 0$, and σ_m^2 equal to 10% of the trait's initial genotypic variance/$2L$ (see table A1).

Reproduction and Survival

Each female produces a number of eggs (R), which are sequentially fertilized at a constant time interval equal to 1 (fig. B1; figs. B1–B4, C1–C3, D1–D5 available online). Between fertilization events, females mate at a constant interval determined by τ. Mating is therefore under full female control (e.g., Parker and Ball 2005; Fromhage et al. 2008). The total mating time equals R; in this time, a female mates $\sim R/\tau$ times, each time with a male randomly selected from the entire population. If $\tau = 1$, a female is effectively monandrous for a single fertilization event (i.e., she mates with a single male for each egg). If $\tau < 1$, a female is polyandrous and mates multiply per egg. Our model constitutes a full-range model (Engqvist and Reinhold 2006; Fromhage et al. 2008; Parker and Pizzari 2010) as the evolving female trait τ determines both the risk and intensity of sperm competition.

Each female mating with a male i receives s_i sperm cells, which subsequently die at rate μ_i. At the time of fertilization ($t = 1, 2, 3 \ldots R$), viable sperm compete for fertilization. The number of viable sperm ζ_i of male i who mated with the female at time t_i is given by

$$\zeta_{i,t} = s_i e^{-\mu_i (t - t_i)} \tag{1}$$

(Parker 1998; Engqvist 2012).

The fertilization probability of male i (φ_i, where i represents the male's mating order among the female's mates, N_{mates}) is determined by a lottery between his viable sperm and those of the female's other mates:

$$\varphi_i = \frac{\alpha^i \zeta_i}{\sum_{j=1}^{N_{\text{mates}}} \alpha^j \zeta_j} \tag{2}$$

(cf. Engqvist and Reinhold 2006).

Here, α is the loading factor determining the lottery type; $\alpha = 1$ gives a fair raffle (cf. Engqvist 2012), where each male's fertilization probability is directly proportional to its amount of viable sperm with no bias. This terminology differs somewhat from classical definitions of fair raffle (Parker and Pizzari 2010), since a male's fertilization probability depends on his sperm longevity as well as initial number. Given ejaculates of equal sperm number and longevity, there is therefore last-male advantage, akin to a raffle with passive loss (i.e., a specific form of loaded raffle; Lessells and Birkhead 1990; Parker and Pizzari 2010). Here, sperm mortality is constant across males, but in our model, μ is an evolving male trait. When $\alpha \neq 1$, paternity bias depends on male mating order; $\alpha > 1$ and $\alpha < 1$ bias paternity toward the last and first male to mate, respectively (Engqvist and Reinhold 2006).

We impose female sperm limitation by modeling the probability of egg fertilization (Φ) as a function of the total viable sperm available to the female at the time of fertilization (Z_t):

$$\Phi_t = 1 - e^{-rZ_t}. \tag{3}$$

Here, r is the probability that each sperm cell will fertilize the egg if it is not already fertilized and represents the relative number of sperm required for fertilization (Schwartz et al. 1981; Alonzo and Pizzari 2013). The female's total sperm Z_t may comprise viable sperm from multiple males, including any remaining from previous fertilization events.

In the absence of direct fitness costs of the three focal traits (τ, s, and μ), both females and males have a survival probability of 1 throughout the R sequential fertilization events. When costs exist, individual survival probability, ψ_i, decreases with time:

$$\psi_{i,t} = e^{(\ln(v_i)/R)t}. \tag{4}$$

Here, v_i is the individual viability as defined by sex-specific costs applied through direct selection toward a naturally selected optimum (Lande 1981; Bulmer 1989). We define v_i as the probability that the individual will be alive at time $t = R$, and hence the individual's mortality rate throughout the R sequential fertilization events is $-\ln(v_i)/R$. Individual mortality occurs after each possible fertilization event (fig. B1). Given a cost of female mating, female i's viability is

$$v_i = e^{-(R/\tau)^2/2\omega_f^2}, \tag{5}$$

where ω_f is the strength of direct selection (higher values represent weaker selection) on female mating. A female's survival probability at time t ($\psi_{i,t}$), therefore, depends on the number of matings taken so far, which equals the expected number of matings at time t given the female genotype (τ).

Males have a maximum amount of resources, ρ_0, to allocate to sperm traits without paying any survival cost. Allocating more resources imposes a cost such that the viability of male i is given by

$$v_i = \begin{cases} e^{-(\rho_i - \rho_0)^2/2\omega_m^2} & \rho_i > \rho_0 \\ 1 & \rho_i \leq \rho_0 \end{cases}, \tag{6}$$

where ω_m is the strength of direct selection on male investment in sperm (fig. B2). The total amount of resources allocated to sperm, ρ_i, is determined by male investment in s and μ. We assume a trade-off between s and μ following Engqvist (2012):

$$\rho_i = s_i \beta \left(\frac{1}{\mu_i}\right)^a. \tag{7}$$

Here, β is a scaling parameter that determines the cost of a single sperm cell (fig. B3), and a determines the trade-off shape, where the cost of sperm is a decelerating ($a < 1$), linear ($a = 1$), or accelerating ($a > 1$) function of sperm longevity ($1/\mu$; Engqvist 2012). Higher a corresponds to higher cost of sperm longevity but lower cost of increasing sperm number at the expense of sperm longevity compared to lower a (fig. B4). We do not explicitly impose positive genetic covariance between s and μ, but this emerges from the model due to the assumed trade-off (fig. D3–D5).

After reproduction, all adults die and offspring undergo density-dependent mortality. The survival probability of each offspring is given by $\min(K/N_{\text{off}}, 1)$, where K is the population carrying capacity and N_{off} is the total number of offspring.

Simulations

We initially ran simulations, where μ and s but not τ could evolve, to verify that our basic model reproduced Engqvist's (2012) numerical results (app. C; apps. B–D available online). We then allowed all three traits to evolve. We ran series of simulations where (*a*) there is no female sperm limitation (i.e., eq. [3] does not apply and $\Phi = 1$, as long as the female has one viable sperm cell), polyandry has variable direct cost (no cost, $\omega_f^2 = 2.56 \times 10^5$, 1.28×10^5, and 6.4×10^4), and sperm has a constant direct cost ($\omega_m^2 = 1$); and (*b*) females are sperm limited (sperm fertilization efficiency, $r = 0.015$, corresponding to ~300 sperm cells for $\Phi = 0.99$), polyandry and sperm are costly ($\omega_f^2 = 1.28 \times 10^5$, $\omega_m^2 = 1$), and the cost of single sperm cells is varied ($\beta = 0.001, 0.0015, 0.002, 0.0025, 0.003$). We thereby test the key hypotheses that female sperm limitation in combination with dynamics of male allocation to sperm traits can maintain polyandry, even given negative direct selection, and that male allocation dynamics under sperm competition can maintain sperm limitation, therefore creating positive selection for polyandry.

For the latter parameterization, when $\beta < 0.002$, there exists parameter space for μ and s in which males can deliver sufficient viable sperm to ensure fertilization ($\Phi \approx 1$) of a monandrous female without paying any survival cost (fig. B3). For $\beta \geq 0.002$, this is not possible, and males must pay a survival cost (which increases with β) to ensure full fertility of a monandrous female. Hence, the parameterizations of β and r, although arbitrary in absolute terms, are relevant relative to each other. Here, sperm is cheap relative to sperm limitation when $\beta < 0.002$, expensive when $\beta > 0.002$, and on the edge between cheap and expensive when $\beta = 0.002$ (i.e., males can provide sufficient viable sperm to fertilize a monandrous female by paying no, substantial, or a small survival cost, respectively). Since varying β effectively corresponds to varying the level of sperm limitation, it is redundant to run simulations where r is varied. We also explored the influence of the shape of the trade-off between s and μ ($a = 0.5$, 1, and 2) on the evolution of μ, s, and τ.

For the above simulations, we assumed fertilization followed a fair raffle (Parker 1990) weighted by each male's number of viable sperm ($\alpha = 1$). We then relaxed this assumption and quantified effects of different forms of sperm competition (loaded raffle; $\alpha = 0.1, 0.5, 2, 10$; cf. Engqvist and Reinhold 2006). Finally, we quantified effects of nonzero environmental variance in sperm traits by running simulations with $\varepsilon = 0.1$ and 1, corresponding to initial heritabilities of s and μ of 0.9 and 0.5, respectively. Because of the decrease in the genetic variance due to drift and selection, the equilibrium heritabilities were much lower and, hence, realistic (Reeve 2000; Simmons and Moore 2009).

For all simulations, we initialized the population at carrying capacity $K = 1{,}250$ individuals, 1:1 sex ratio, and constant female fecundity $R = 8$. We assigned a random genome to each individual: each allele was sampled from normal distributions with set initial mean and variance. Each simulation was run for 50 replicates, and each replicate was run for 10,000 generations to reach equilibria. All parameters are summarized in table A1. Means are presented ± standard deviation. The model source code is deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.3mh3c (Bocedi et al. 2016).

Results

Evolution of Polyandry When Females Are Not Sperm Limited

Simulations investigating the evolution of male allocation to sperm number (s) and mortality rate (μ) under fixed polyandry closely matched Engqvist's (2012) numerical results (app. C). When we also allowed female mating interval (τ) to evolve, there was evidence that τ, μ, and s coevolved as predicted (fig. 1). With no direct selection against polyandry, τ reached equilibria anywhere between the imposed limits of 0.01 and 1.0, presumably depending on the direction of initial drift (fig. 1*A*). In individual simulations where females evolved to be monandrous ($\tau = 1$), males evolved low μ and s, such that a single male that mated with a female at the start of the mating interval would provide enough viable sperm for fertilization (fig. 1*A*, black lines). When some polyandry persisted ($\tau < 1$), males evolved correspondingly higher μ and s (fig. 1*A*, gray lines). Because of more polyandry, sperm competition was greater, causing males to invest more in sperm number than longevity (e.g., Engqvist 2012; app. C). Consequently, because sperm longevity was reduced, females had to mate multiply to ensure fertility even when only one sperm cell was required for fertilization. These patterns illustrate that coevolutionary feedbacks can arise between polyandry and male allocation to sperm traits. Even when polyandry is selectively neutral for females, sperm allocation dynamics can drive polyandry to high or low levels, with initial stochasticity directing the system to divergent equilibria (fig. 1*A*).

When polyandry was subjected to negative direct selection (i.e., was costly), females became monandrous in most simulations ($\tau = 1$; figs. 1*B*, D1), especially given higher costs (fig. D1*B*). However, there was again evidence of coevolution between female and male traits, shown by a negative relationship between τ and both s and μ (fig. 1*B*, solid black and gray lines). Polyandry occasionally persisted (figs. 1*B*, gray line, and D1), suggesting that even without sperm limitation, costly polyandry can potentially evolve due to coevolutionary feedbacks with male allocation to sperm.

Evolution of Polyandry When Females Are Sperm Limited

Our primary hypothesis was that, given female sperm limitation, feedbacks between male allocation to s versus μ and female τ might maintain costly polyandry. Indeed, introducing female sperm limitation caused costly polyandry to be maintained to a degree that depended on the cost of sperm and, hence, on male allocation dynamics (figs. 2, D2).

Given a linear trade-off between s and $1/\mu$ ($a = 1$; fig. 2, gray boxes), when sperm was cheap relative to sperm limitation ($\beta < 0.002$), females typically evolved to be monandrous ($\tau = 1$; fig. 2*A*). Males evolved relatively low μ (fig. 2*B*) and could ensure fertilization (figs. 2*D*, 3*A*). However, some polyandry occasionally evolved and persisted, as in the simulations with no sperm limitation (cf. figs. 2*A*, 1*B*).

In contrast, when sperm was expensive relative to sperm limitation ($\beta > 0.002$), males evolved higher μ (fig. 2*B*) but similar or lower s (fig. 2*C*) than when $\beta < 0.002$, providing monandrous females with mean fertilization probability

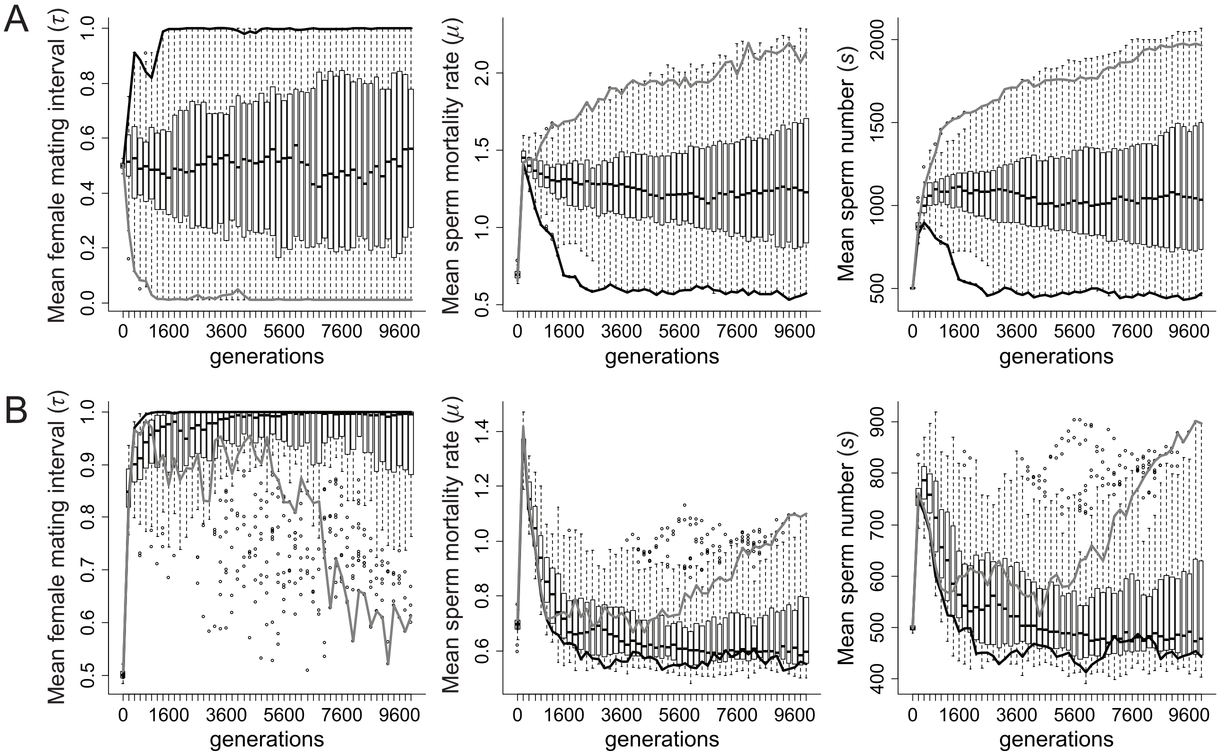

Figure 1: Evolution of female mating interval (τ) and male sperm mortality rate (μ) and sperm number (s) when females are not sperm limited and there is no direct cost on polyandry (*A*) or polyandry imposes a direct cost on female survival (*B*; strength of selection on female mating $\omega_f^2 = 1.28 \times 10^5$; see fig. D1 for other values), given cost of sperm $\beta = 0.002$, shape of trade-off $a = 1$, and strength of selection on male allocation to sperm $\omega_m^2 = 1$. Mean population τ, μ, and s are shown as median (solid bands), first and third quartiles (box limits), and approximately twice the standard deviation (whiskers) over 50 replicate simulations, at 200-generation intervals. The solid lines depict two representative runs where females evolved to be monandrous ($\tau = 1$; black lines) or polyandrous ($\tau < 1$; gray lines).

$\Phi = 0.945 \pm 0.004$ (figs. 2*D*, 3*G*). Some polyandry consequently evolved (fig. 2*A*), albeit little because of the direct cost. In turn, polyandry increased sperm competition and, hence, reduced sperm longevity, triggering coevolutionary feedbacks that kept the system in equilibrium. Therefore, the balance between the cost of sperm (β) and sperm limitation appears to be key in shaping coevolution between polyandry and allocation to sperm traits.

Figure 3 illustrates the underlying mechanism. If sperm is cheap relative to sperm limitation ($\beta < 0.002$), males can easily evolve to ensure fertilization of a monandrous female without paying much or any survival cost (fig. 3*A*, 3*B*). Hence, a male who provided lower Φ would have no advantage of paying a lower cost and would fertilize fewer eggs. Conversely, if sperm is expensive ($\beta > 0.002$), males cannot evolve to ensure fertilization to a monandrous female without paying a substantial survival cost (fig. 3*G*, 3*H*). Meanwhile, males that invest less in sperm pay a low or no survival cost and consequently have a higher probability of surviving throughout the reproductive phase. However, they typically cannot provide sufficient viable sperm to fertilize a monandrous female, causing selection for increased polyandry. Because some females mate multiply, males can ensure some paternity without, on average, paying a high cost, and very costly sperm traits are not maintained. A coevolutionary equilibrium is therefore maintained.

The situation where sperm is on the edge of being too costly relative to sperm limitation ($\beta = 0.002$; fig. 2, gray shaded area, and fig. 3*D*–3*F*) provides a useful illustration. Here, males fertilized a monandrous female with mean probability $\Phi = 0.98 \pm 0.003$ (fig. 2*D*), yet some polyandry was maintained (fig. 2*A*; mean $\tau = 0.8 \pm 0.13$, for $a = 1$). Although the mean probability that a monandrous female would remain unfertilized was only 0.02, a proportion of males persisted whose sperm trait combinations meant that they provided a considerably lower Φ (fig. 3*D*). Such males persisted because of the relationship between sperm cost and sperm limitation. Potentially, males could evolve to provide enough viable sperm to fertilize monandrous females while paying relatively little survival cost. However, males that do not provide enough sperm have the advan-

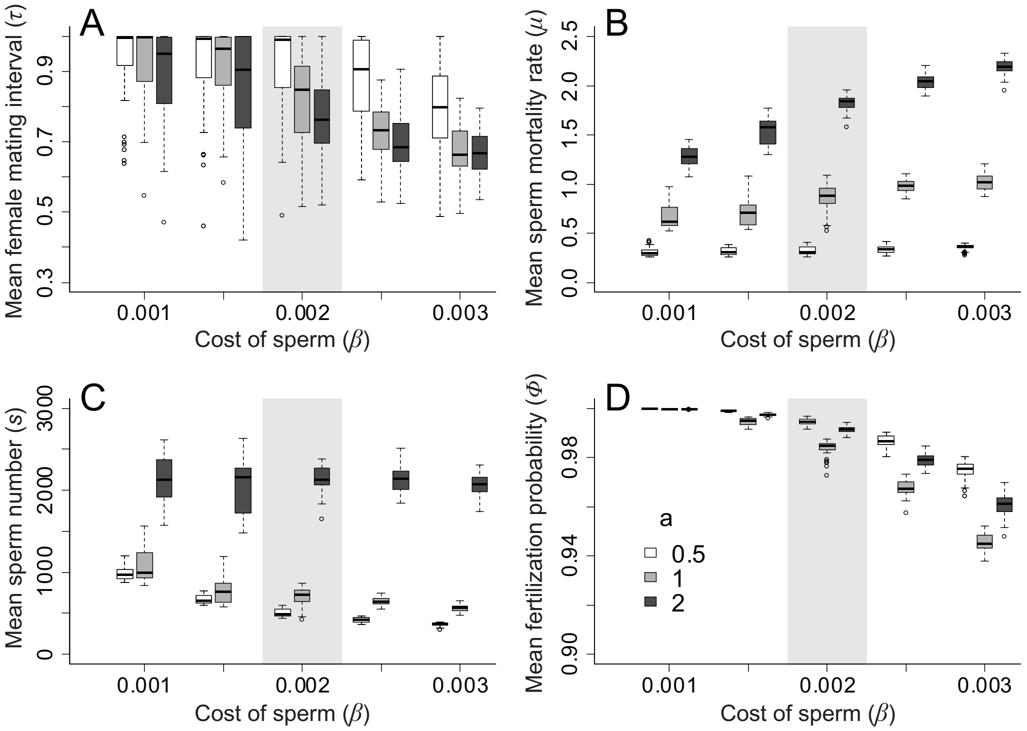

Figure 2: Evolution of female mating interval (τ; *A*), sperm mortality rate (μ; *B*) and sperm number (s; *C*) when females are sperm limited (sperm fertilization efficiency, $r = 0.015$), given different costs of sperm (β), for three different shapes of trade-off between μ and s (a). The cost of sperm is a decelerating ($a = 0.5$; white boxes), linear ($a = 1$; gray boxes), or accelerating ($a = 2$; dark gray boxes) function of sperm longevity ($1/\mu$). *D*, Mean fertilization probability (Φ) for a monandrous female. In all cases, strength of selection on female mating $\omega_{\mathrm{f}}^2 = 1.28 \times 10^5$ and on male allocation to sperm $\omega_{\mathrm{m}}^2 = 1$. Mean population phenotypic values at generation 10,000 are represented as median (solid bands), first and third quartiles (box limits), and approximately twice the standard deviation (whiskers) over 50 replicate simulations.

tage of not paying any cost (fig. 3*D*–3*F*). The balance between cost and fertilization probability is such that the number of offspring sired by males with the latter strategy on average does not differ from, or is even higher than, the number sired by males that invest more in sperm (fig. 3*F*). Therefore, as long as some females mate multiply, alleles underlying sperm traits that translate into lower Φ can increase in frequency, maintaining sperm limitation and creating selection for increased polyandry.

The shape of the trade-off between s and μ affected the evolution of τ when sperm was relatively costly ($\beta \geq 0.002$; fig. 2*A*). When $a \geq 1$, s and μ increased (fig. 2*B*, 2*C*), leading to lower Φ than when $a = 0.5$ (fig. 2*D*). This, in turn, caused selection for lower τ (fig. 2*A*). In contrast, when $a = 0.5$, evolution of relatively low μ ensured higher Φ, especially for lower costs of sperm, reducing evolution of polyandry.

Effect of the Form of Sperm Competition

The evolutionary trajectories of τ, μ, and s were affected by the form of sperm competition (fig. 4). Generally, biasing fertilization toward either the first or last male to mate ($\alpha \neq 1$) caused τ to decrease (i.e., more polyandry; fig. 4*A*), especially when sperm was costly relative to sperm limitation ($\beta \geq 0.002$). However, the effects of first-male versus last-male precedence on μ, s, and τ differed.

Given last-male precedence ($\alpha = 2$ and 10), males evolved higher s and consequently higher μ (fig. 4*B*, 4*C*), and the total resources invested in sperm decreased (fig. 4*D*; e.g., Engqvist and Reinhold 2006; Parker and Pizzari 2010). As males that mated last were intrinsically favored, there was reduced selection for high sperm longevity. Last-male precedence also decreased sperm competition, thereby reducing selection for higher s. Consequently, males could not, on average, provide high fertilization probability to monandrous females, causing an evolutionary reduction in τ (fig. 4*F*).

In contrast, given first-male precedence ($\alpha = 0.1$ and 0.5), males evolved lower μ and consequently lower s (fig. 4*B*, 4*C*). This resulted from strong selection for sperm longevity because males needed to provide some viable sperm at the moment of fertilization in order to participate in sperm competition and realize their intrinsic first-male

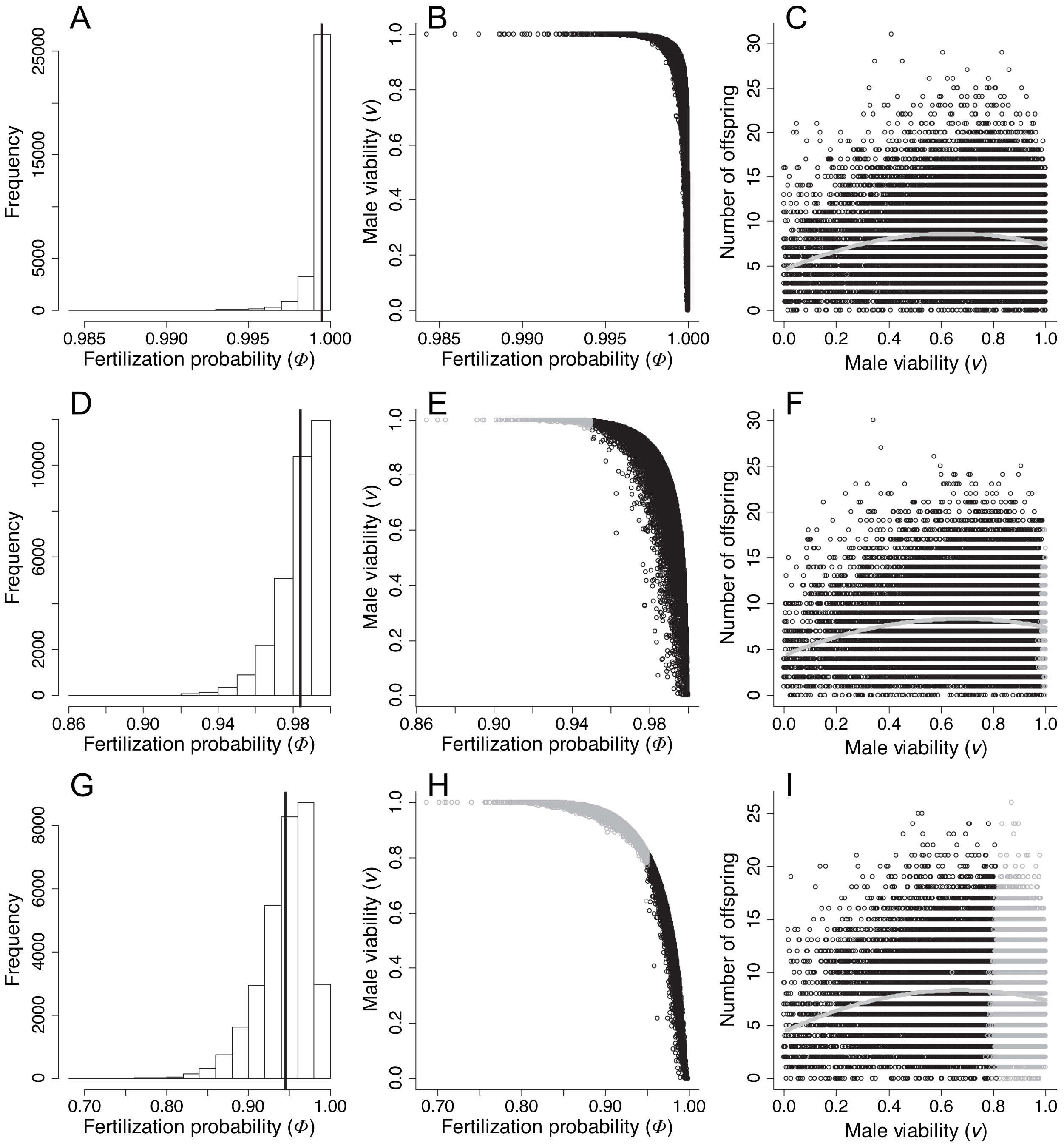

Figure 3: Distribution of the fertilization probability (Φ) a male can ensure to a monandrous female evolving under female sperm limitation (sperm fertilization efficiency, $r = 0.015$), for different costs of sperm (β). *A–C*, $\beta = 0.001$; *D–F*, $\beta = 0.002$; *G–I*, $\beta = 0.003$. *A*, *D*, *G*, Histograms show the distribution of Φ. Black solid lines show the distribution mean. *B*, *E*, *H*, Male viability (v; eq. [6]) as a function of the fertilization probability he can provide to a monandrous female. Each dot represents an individual male. *C*, *F*, *I*, Relationship between a male's viability and the number of offspring sired. Gray and black dots represent individual males that provide less and more than $\Phi = 0.95$, respectively. This threshold is arbitrary, chosen only for illustration purposes. The gray lines represent the quadratic regression of males' number of offspring on male viability ($N_{\text{off},i} \sim v_i + v_i^2$). Plotted data refer to generation 10,000, pooled across 50 replicate simulations with strength of selection on female mating $\omega_{\text{f}}^2 = 1.28 \times 10^5$ and on male allocation to sperm $\omega_{\text{m}}^2 = 1$, and $a = 1$. Note that, for clarity, *X*-axes are on different scales.

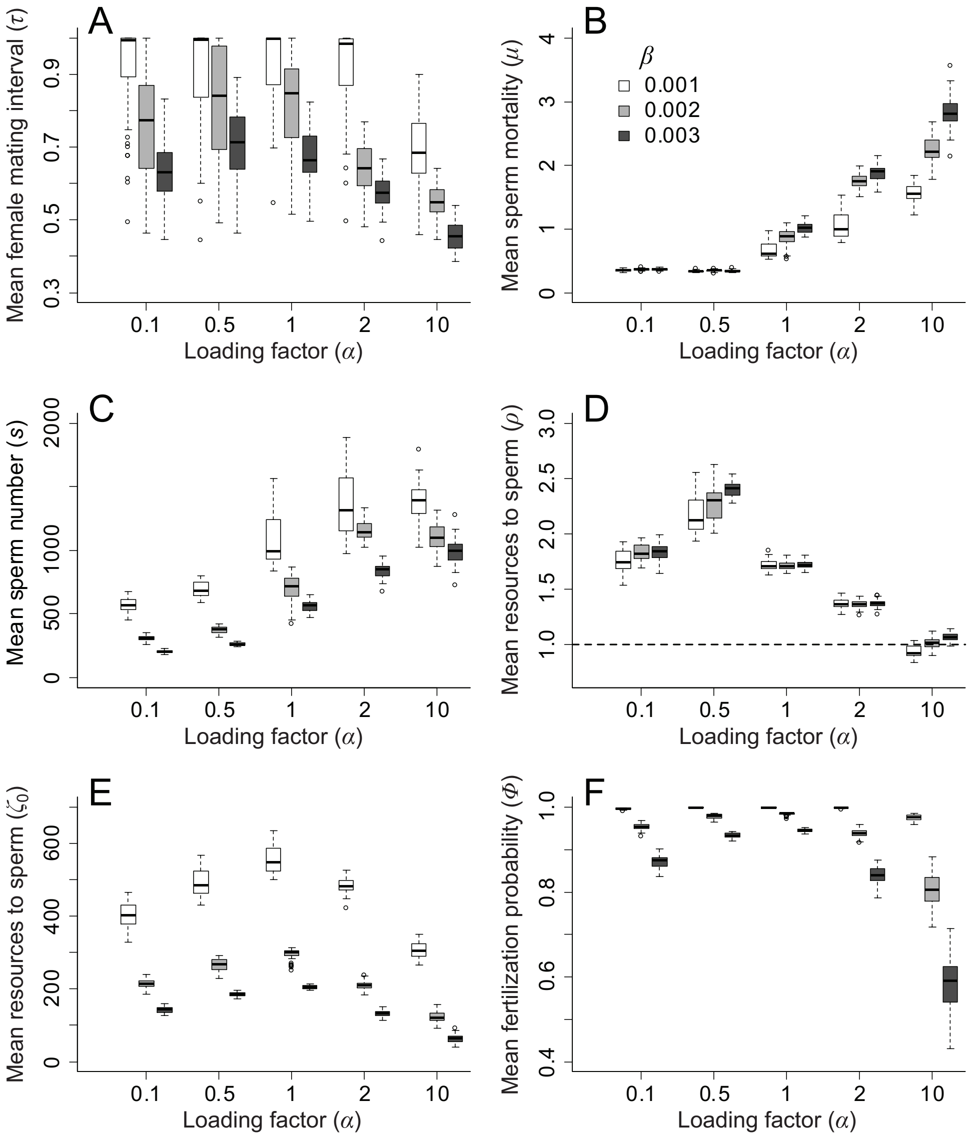

Figure 4: Evolution of female mating interval (τ; *A*), sperm mortality rate (μ; *B*), and sperm number (s; *C*) when females are sperm limited (sperm fertilization efficiency, $r = 0.015$), under different forms of sperm competition (a), for three different costs of sperm: $\beta = 0.001$ (white boxes), $\beta = 0.002$ (gray boxes), and $\beta = 0.003$ (dark gray boxes). *D*, Mean resources invested in sperm (ρ). The dashed line shows $\rho_0 = 1$, that is, the limit above which males pay a survival cost for allocation to sperm. *E*, Mean viable sperm at fertilization of the first male to mate with the females (ζ_0; i.e., mean viable sperm available to a monandrous female). *F*, Mean fertilization probability (Φ) for a monandrous female. In all cases, strength of selection on female mating $\omega_f^2 = 1.28 \times 10^5$ and on male allocation to sperm $\omega_m^2 = 1$, and $a = 1$. Mean population phenotypic values at generation 10,000 are represented as median (solid bands), first and third quartiles (box limits), and approximately twice the standard deviation (whiskers) over 50 replicate simulations.

advantage. Furthermore, decreased μ meant that more sperm survived to the time of fertilization than given last-male precedence (fig. 4*E*). Sperm competition consequently increased, especially for $\alpha = 0.5$, causing males to invest more resources in sperm (fig. 4*D*). This, in turn, increased Φ for monandrous females (fig. 4*F*) and, hence, increased τ compared to last-male precedence. Indeed, when sperm was relatively cheap ($\beta = 0.001$), first-male precedence did not (on average) lead to evolution of polyandry (fig. 4*A*), as given a fair raffle.

Effect of Environmental Variance in Sperm Traits

Introducing environmental variance in sperm phenotypes caused evolution of higher s, higher μ, and lower τ (i.e., more polyandry; fig. 5*A*–5*C*). The evolutionary increase in

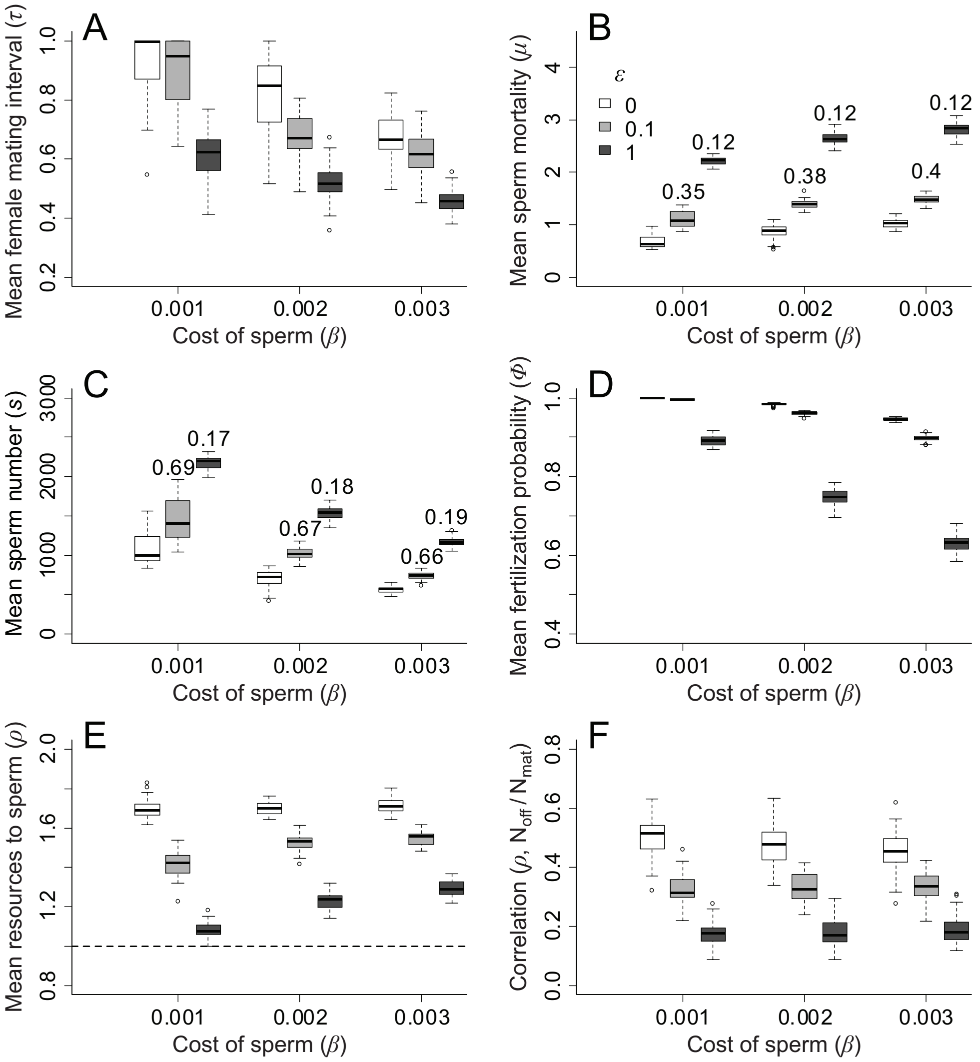

Figure 5: Effect of nonzero environmental variance in sperm traits on the evolution of female mating interval (τ; *A*), sperm mortality rate (μ; *B*), and sperm number (s; *C*) when females are sperm limited (sperm fertilization efficiency, $r = 0.015$), across different costs of sperm (β). White boxes indicate $\varepsilon = 0$ (i.e., zero environmental variance), gray boxes indicate $\varepsilon = 0.1$, and dark gray boxes indicate $\varepsilon = 1.0$. *D*, Mean fertilization probability (Φ) for a monandrous female. *E*, Mean resources invested in sperm (ρ) calculated from the genotypic values of s and μ (i.e., prior to the effect of environmental variance). The dashed line shows $\rho = 1$, that is, the limit above which males pay a survival cost for allocation to sperm. *F*, Correlation between resources invested in sperm (ρ; calculated as in *D*) and male reproductive success expressed as a male's number of offspring (N_{off}) divided by his number of matings (N_{mat}). In all cases, strength of selection on female mating $\omega_{\mathrm{f}}^2 = 1.28 \times 10^5$ and on male allocation to sperm $\omega_{\mathrm{m}}^2 = 1$, $a = 1$, and raffle loading factor $\alpha = 1$. Mean population phenotypic values at generation 10,000 are represented as median (solid bands), first and third quartiles (box limits), and approximately twice the standard deviation (whiskers) over 50 replicate simulations. Numbers in *B* and *C* show the mean heritabilities of μ and s, respectively, at generation 10,000. Heritability $h^2 = 1$ when $\varepsilon = 0$.

s might arise because males need to buffer against possible reductions in s due to negative environmental deviations and against competition with males whose s was increased by a positive environmental deviation. Even stronger positive selection on s might then arise than when there is no environmental variation. Due to the trade-off between s and μ, males can increase s without paying a high survival cost only by increasing μ. Furthermore, because of the specified form of trade-off (following Engqvist 2012), male survival cost increases linearly with increasing s but exponentially with increasing μ. A given environmentally induced reduction in μ, therefore, causes a higher cost than a comparable environmentally induced increase in s. The evolutionary increase in μ might, therefore, arise because males need to buffer against a high environmentally induced survival cost.

For a given cost of sperm (β), increasing environmental variance decreased the resources that males allocated to sperm (ρ; fig. 5*E*). This is because higher environmental variance reduced the probability that a male with relatively high ρ would win competition for fertilization, meaning that the benefit of high ρ does not outweigh the high associated survival cost. Meanwhile, a genotype that gives high ρ might pay too high a survival cost due to environmental variation in μ. These mechanisms caused a decreased correlation between ρ and male reproductive success given increasing environmental variance in s and μ (fig. 5*F*) and a consequent reduction in ρ. Consequently, the average fertilization probability for a monandrous female decreased (fig. 5*D*), driving increased polyandry.

Our parameter values meant that the equilibrium heritabilities of sperm traits were in line with recent empirical estimates and matched the observation that h^2 of sperm number is usually higher than that of traits related to sperm viability (Simmons and Moore 2009). For example, $\beta = 0.002$ and $\varepsilon = 0.1$ gave equilibrium $h^2 = 0.67 \pm 0.06$ for s and 0.38 ± 0.04 for μ, while $\varepsilon = 1.0$ gave $h^2 = 0.18 \pm 0.04$ for s and 0.12 ± 0.02 for μ.

Discussion

One broad hypothesis explaining the evolution of costly polyandry is that female mating rate might coevolve with male reproductive strategy (Keller and Reeve 1995; Engqvist 2012; Alonzo and Pizzari 2013; Abe and Kamimura 2015; Bocedi and Reid 2015). Specifically, increased sperm competition stemming from increased polyandry has been suggested to drive evolution of increased sperm number at a cost of reduced sperm longevity (Engqvist 2012). The resulting low sperm viability might create female sperm limitation, causing females to mate multiply to ensure fertilization. The consequent increased sperm competition would cause further evolutionary reductions in sperm longevity, driving a coevolutionary feedback loop that further increases female mating rate (Engqvist 2012; Alonzo and Pizzari 2013).

To test this hypothesis, we built an IBM where male allocation to sperm number and sperm longevity as well as female mating interval can all evolve. Our model shows that the hypothesized coevolutionary feedbacks can occur and drive evolution of polyandry under a range of conditions, even given negative direct selection. The balance between the cost of sperm and the degree of female sperm limitation underpins such feedbacks. If sperm is costly relative to sperm limitation, a proportion of males produce insufficient viable sperm to guarantee fertilization of a monandrous female. Since such males do not pay any survival cost and will fertilize some eggs of polyandrous females, alleles underlying such trait values are maintained, in turn maintaining alleles that underlie female multiple mating and consequent sperm competition.

Abe and Kamimura (2015) demonstrated similar coevolutionary dynamics in a model where female mating frequency and male sperm number, but not sperm longevity, evolved given a trade-off between investment in sperm and mate acquisition (i.e., between post- and precopulatory traits). They modeled sperm limitation by varying the operational sex ratio from equal to female biased and by varying sperm fertilization efficiency (equivalent to our r). Congruent with our own results, Abe and Kamimura (2015) found that females evolve to be more polyandrous with increasing sperm limitation, but the mechanism is completely different. In Abe and Kamimura's (2015) model, sperm limitation is reinforced because males reduce their investment in sperm number to increase their number of matings. In contrast, our model does not explicitly consider any precopulatory male trait; overall mating frequencies are primarily determined by female mating rate τ. A male's number of matings does vary to some degree with his genotype: as a male invests more in higher sperm number or longevity, his survival probability across successive mating intervals decreases, decreasing his number of matings. However, the coevolutionary dynamics that emerge in our model are induced by the two postcopulatory traits: sperm number and longevity. As sperm become more expensive relative to sperm limitation, males evolve lower sperm longevity, but sperm number does not decrease. Polyandry is therefore maintained because of reduced sperm viability, reinforced by increasing polyandry and high cost of sperm, not because of reduced sperm number. Our IBM approach also highlights a novel dimension: the importance of among-male variation in allocation to sperm. The persistence of some males that do not pay any survival cost because they invest less in sperm but cannot guarantee fertilization of monandrous females creates ongoing sperm limitation and, hence, selection for polyandry without need for exterior forces such as biased sex ratios.

Fertilization assurance has previously been proposed to explain polyandry but has perhaps been underemphasized because sperm are commonly assumed to be sufficiently numerous to ensure fertilization. Fertilization assurance can be considered a direct benefit of polyandry, exerting positive direct selection (Sheldon 1994; Arnqvist and Nilsson 2000; Uller and Olsson 2005; Hasson and Stone 2009; Friesen et al. 2014*b*; Snook 2014). However, the classic fertilization assurance hypothesis does not explain why females should be sperm limited in the first place. Our model demonstrates that sperm limitation can itself be caused and reinforced by polyandry, because polyandry causes sperm competition and drives evolution of sperm traits, preventing males from evolving to overcome female sperm limitation. Indeed, the fact that two very different models (ours and that of Abe and Kamimura 2015) conclude that evolutionary feedbacks between female mating rate and male pre- and/or postcopulatory traits can promote evolution of costly polyandry indicates that there are multiple, potentially interacting processes that can influence the coevolutionary dynamics of male and female strategies in the presence of sperm limitation, adding new dimensions to the fertilization assurance hypothesis. By maintaining sperm limitation, sperm competition exerts positive direct selection on female multiple mating, and the evolution of polyandry does not rely on genetic covariance with male traits (which was effectively zero in our simulations; figs. D3–D5; cf. Keller and Reeve 1995; Bocedi and Reid 2015).

Sperm Limitation and Costs

Our model and the emergent coevolutionary feedbacks rely on two key assumptions: females are sperm limited, and sperm are costly relative to that limitation. To evaluate the general relevance of our results, we therefore need to evaluate these assumptions. First, how common is female sperm limitation in nature? There is increasing evidence that female sperm limitation occurs and can be caused by diverse mechanisms, such as male sperm allocation, sperm depletion, and partial infertility (Warner et al. 1995; Jones 2001; Preston et al. 2001; Wedell et al. 2002; García-González 2004; Kraus et al. 2004; Dean et al. 2010; Alonzo and Pizzari 2013; Boivin 2013; Friesen et al. 2014*a*, 2014*b*). For internal fertilizing species, Hasson and Stone's (2009) mathematical model showed that male infertility caused by oligospermy could potentially maintain costly female extra-pair mating in socially monogamous species. Interestingly, oligospermy, or male infertility, more generally, might be common in nature due to antagonistic coevolution between males and females stemming from the conflicting interests of males to increase fertilization efficiency and females to reduce the risk of polyspermy (Eberhard 1996; Morrow et al. 2002; Hasson and Stone 2009). Furthermore, resistance to harmful sperm, filtering for higher-quality sperm, and cryptic female choice have been shown or hypothesized to promote the evolution of female reproductive tracts that are highly hostile to sperm cells (e.g., Birkhead et al. 1993; Holland and Rice 1999). Female sperm limitation might, therefore, result from the high mortality and loss of sperm due to female adaptation.

Second, might sperm be sufficiently costly to generate and maintain female sperm limitation? Indeed, it is plausible that the combination of costly sperm (Dewsbury 1982; Nakatsuru and Kramer 1982; Pitnick et al. 2009) and the continuous arms race between female reproductive tract and male ejaculate (Birkhead et al. 1993; Hasson and Stone 2009) could maintain the system at the edge between female sperm limitation and males producing enough viable sperm to fertilize a monandrous females. Other common causes of male partial infertility that do not directly depend on male strategy include deleterious mutations (Blumenstiel 2007), antagonistic selection on mitochondrial genes (Hasson and Stone 2009; Yee et al. 2013; Padua et al. 2014), and inbreeding depression (Losdat et al. 2014). Such mechanisms might further increase female sperm limitation and cost of sperm if males must invest more to counterbalance the reduced fertilizing efficiency of their sperm, making the assumption of costly sperm relative to sperm limitation plausible.

Form of Sperm Competition

Our model shows that coevolutionary feedbacks between polyandry and allocation to sperm traits depend on the form of sperm competition. Our results support Engqvist's (2012) hypothesis that sperm longevity will decrease, moving from first-male precedence to fair raffle to last-male precedence. Previous models that considered sperm number but not longevity predicted that sperm number (also interpretable as male investment in sperm) would be lower given a loaded raffle but would not depend on the direction of precedence (Fromhage et al. 2008). Engqvist and Reinhold (2006) also predicted no difference in resource allocation to sperm given first-male versus last-male precedence under high risk or low intensity of sperm competition (i.e., low female mating frequency) but predicted increasing allocation to sperm given last-male versus first-male precedence under high intensity of sperm competition (i.e., high female mating frequency). In contrast, in our model, which remains in the range of high risk and low intensity of sperm competition, sperm number decreased with first-male precedence but increased with last-male precedence. This reflects increased selection for sperm longevity given first-male precedence and the trade-off between sperm longevity and number. The total resources allocated to sperm decreased with increasing last-male precedence but increased with intermediate first-male precedence and were comparable to fair raffle in the case of strong first-male precedence. Because of the increased sperm longevity given first-male precedence, males were likely to experience more intense sperm competition, explaining the increased resource allocation. Considering the simultaneous evolution of sperm number and longevity, therefore, adds complexity to the simple predictions made by previous models of maximum ejaculate investment under fair-raffle fertilization (Parker and Pizzari 2010).

Fair-raffle fertilization appears to be widespread in nature (Gage and Morrow 2003; Engqvist et al. 2007; Manier et al. 2010; Simmons 2014) and might be expected in internal fertilizers where females are not limited for sperm storage capacity. However, for species where capacity is constrained (e.g., many insects; Parker and Pizzari 2010), sperm competition appears to follow a heavily loaded raffle (Simmons and Siva-Jothy 1998; Parker and Pizzari 2010; Simmons 2014). The feedback dynamics that emerged in our model might, therefore, be particularly important in maintaining polyandry in such species, but specific evolutionary predictions will depend on the form of male precedence.

Environmental Variance in Sperm Traits

Previous models of polyandry evolution and allocation to sperm traits are typically not genetically explicit and implicitly assume a heritability of 1 for key traits (e.g., Parker and Ball 2005; Fromhage et al. 2008; Engqvist 2012; Alonzo and Pizzari 2013). However, this assumption is unrealistic; heritabilities of traits that are closely related to fitness, including traits influencing fertilization, are typically considerably less than 1 (Mousseau and Roff 1987; Houle 1992). Moderate heritability has been estimated for traits related to sperm number (commonly $0.2 \leq h^2 \leq 0.5$), while heritabilities of traits related to sperm performance are typically lower ($0.1 \leq h^2 \leq 0.4$; Simmons and Moore 2009; Chargé et al. 2013). The assumption of a substantial additive genetic basis to key traits is critical for many models regarding mating system evolution and sexual selection, where relaxing the assumption of $h^2 = 1$ can influence predictions or even completely eliminate the postulated mechanisms (Roff and Fairbairn 2014; Bocedi and Reid 2015). Our model shows that increasing the environmental variance in sperm number and mortality rate, and, hence, reducing h^2, might actually facilitate coevolution of polyandry and male allocation to ejaculate traits. Underlying mechanisms and resulting evolutionary dynamics could be complex, and further investigation is required to quantify resulting components of selection and their dependence on the scale and form of modeled traits and trade-offs and the effects of environmental variance in female mating rate itself.

Model Assumptions and Extensions

Our model provides an important advance because it explicitly considers dynamic coevolutionary feedbacks between female mating interval and male allocation to competing sperm traits. However, it makes simplifying assumptions that future modeling should relax. We assumed that males mate with females at time intervals that are fixed and uniform within each female. However, males might potentially evolve to mate at a time that maximizes their fertilization success (Huck et al. 1989). Male competition for mating might then be stronger closer to fertilization, possibly causing even stronger postcopulatory competition for fertilization. Sperm longevity might then be less important in maintaining polyandry than other pre- and postcopulatory traits involved in other trade-offs. Moreover, the evolution of such male strategies would cause females to cede complete control of mating, potentially changing the evolution of allocation to sperm traits (Williams et al. 2005; Fromhage et al. 2008).

We also assumed that males replenish their sperm resources after each mating and that males can mate unlimited times. Alternatively, males could have a certain resource budget to allocate to reproduction per lifetime or per reproductive season (Preston et al. 2001; Boivin 2013; Friesen et al. 2014*a*) and evolve differential allocation to different ejaculates (Wedell et al. 2002; Pizzari et al. 2003; Katvala et al. 2008; Parker and Pizzari 2010; Kelly and Jennions 2011). Under sperm competition and fixed resource budget, males are expected to invest more sperm in each single ejaculate (Parker and Pizzari 2010) and in initial copulations at the expenses of future possible ones (Reinhold et al. 2002), possibly leading to further sperm limitation because of sperm depletion (Härdling et al. 2008).

Finally, a fundamental assumption of our model is the existence of a sperm number/longevity trade-off (Moore et al. 2004; Snook 2005), and more empirical data are required to quantify the form of such trade-offs in nature. Furthermore, males likely allocate resources among more than these two ejaculate traits (Snook 2005) and among pre- and postcopulatory processes (Katvala et al. 2008; Evans 2010; Engqvist 2011; Kvarnemo and Simmons 2013; Lüpold et al. 2014). Sperm limitation could, therefore, be caused and maintained through complex feedbacks between multiple female and male strategies involving, for example, mate choice (Tazzyman et al. 2009), male mate guarding (Warner et al. 1995; Alonzo and Warner 2000), investment in parental care (Alonzo 2010), or investment in within-pair versus extra-pair mating in socially monogamous species (Hunter et al. 2000; Calhim et al. 2011). Theory has only just started to explicitly consider such complex feedbacks between multiple female and male traits (Abe and Kamimura 2015), providing fertile ground for future development.

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APPENDIX A

Summary of Model Variables and Parameters

Table A1: Summary of variables and parameter values used in the model

Type, variable	Description	Parameter values
General:		
K	Carrying capacity	1,250 individuals
R	Female fecundity	8
r	Fertilization rate	.015
L	No. diploid loci for each trait	20
ζ	No. viable sperm of individual male at time of fertilization	…
φ	Fertilization probability of individual male	…
Z	Total no. viable sperm available to individual female	…
Φ	Egg fertilization probability	…
ψ	Individual survival probability	…
Mutations:		
M	Mutation probability (per allele per generation)	.001
m	Mean mutational effect	.0
σ_m^2	Variance in mutational effects	$.1(\sigma_{\tau,0}^2/2L)$; $.1(\sigma_{s,0}^2/2L)$; $.1(\sigma_{\mu,0}^2/2L)$
Traits:		
g_τ	Female mating interval (genotypic value)	…
g_s	Sperm no. (genotypic value)	…
g_μ	Sperm mortality rate (genotypic value)	…
τ	Female mating interval (phenotypic value)	$.01 \leq \tau \leq 1.0$
s	Sperm no. (phenotypic value)	$g_s + N(0, \varepsilon\sigma_{s,0}^2) \geq 1.0$
μ	Sperm mortality rate (phenotypic value)	$g_\mu + N(0, \varepsilon\sigma_{\mu,0}^2) \geq 10^{-10}$
Traits initialization:		
$\overline{\tau}_0$	Initial genotypic mean for female mating interval	.5
$\bar{s}_0$	Initial genotypic mean for sperm no.	500
$\overline{\mu}_0$	Initial genotypic mean for sperm mortality rate	.5
$\sigma_{\tau,0}^2$	Initial genotypic variance for female mating interval	.1
$\sigma_{s,0}^2$	Initial genotypic variance for sperm no.	10,000.0
$\sigma_{\mu,0}^2$	Initial genotypic variance for sperm mortality rate	1.0
Costs and trade-off:		
ω_{f}^2	Strength of direct selection (cost) for female mating	2.56×10^5, 1.28×10^5, 6.4×10^4
ω_{m}^2	Strength of direct selection (cost) for sperm	1.0
ρ_0	Max. amount resources to allocate to sperm without incurring survival cost	1.0
ρ	Male resource allocation to sperm	…
β	Scaling parameter determining cost of single sperm cell (eq. [7]; fig. B3)	.001, .0015, .002, .0025, .003
a	Shape of sperm no./longevity trade-off (eq. [7]; fig. B4)	.5, .75, 1, 1.5, 2
α	Raffle loading factor	.1, .5, 1, 2, 5, 10
$\varepsilon_s = \varepsilon_\mu$	Proportions of the initial genotypic variance for sperm no. and mortality rate that defines the respective environmental variances	0, .1, 1.0

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