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Sperm competition games: sperm size (mass) and number under raffle and displacement, and the evolution of P_2

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Abstract

We examine models for evolution of sperm size (i.e. mass m) and number (s) under three mechanisms of sperm competition at low 'risk' levels: (i) raffle with no constraint on space available for competing sperm, (ii) direct displacement mainly by seminal fluid, and (iii) direct displacement mainly by sperm mass. Increasing sperm mass increases a sperm's 'competitive weight' against rival sperm through a diminishing returns function, $r(m)$. ESS total ejaculate expenditure (the product m^*s^*) increases in all three models with sperm competition risk, q. If $r(m)$, or ratio $r'(m)/r(m)$, is independent of ESS sperm numbers, ESS sperm mass remains constant, and the sperm mass/number ratio (m^*/s^*) therefore decreases with risk. Dependency of sperm mass on risk can arise if $r(m)$ depends on competing sperm density (sperm number / space available for sperm competition). Such dependencies generate complex relationships between sperm mass and number with risk, depending both on the mechanism and how sperm density affects $r(m)$. While numbers always increase with risk, mass can either increase or decrease, but m^*/s^* typically decreases with risk unless sperm density strongly influences $r(m)$. Where there is no extrinsic loading due to mating order, ESS paternity of the second (i.e. last) male to mate (P_2) under displacement always exceeds 0.5, and increases with risk (in the raffle $P_2 = 0.5$). Caution is needed when seeking evidence for a sperm size-number trade-off. Although size and number trade-off independently against effort spent on acquiring matings, their product, m^*s^*, is invariant or fixed at a given risk level, effectively generating a size-number trade-off. However, unless controlled for the effects of risk, the relation between m^* and s^* can be either positive or negative (a positive relation is usually taken as evidence against a size-number trade-off).

1. Introduction

Postcopulatory sexual selection is potent agent of evolutionary diversification, generating variation in male and female behaviour, morphology, physiology and biochemistry (e.g. Birkhead and Møller 1998, Birkhead et al. 2009). Discerning the relationship between variation in a given trait and competitive male fertilization success (the outcome of sperm competition and cryptic female choice) can be challenging, however, because sperm precedence pattern is an exceptionally complex phenotypic characteristic. How competitive a given male's ejaculate will be may depend upon its ejaculate volume, sperm number, sperm form (e.g. length), sperm behaviour (e.g. swimming speed), sperm longevity, seminal plasma biochemistry, and complex interactions between the ejaculates of competing males and between each male and the female in which the ejaculates compete (reviewed by Pitnick et al. 2009; Pizzari and Parker 2009). Considerable empirical and theoretical attention has been paid to sperm size (mass) and sperm number (Parker 1993), yet we still lack a unifying theory for how these two important male traits relate to one another and to competitive fertilization success. While the selective benefits of ejaculating many sperm when the risk of encountering sperm competition is high are well appreciated (see Parker 1998), the competitive advantages of producing relatively bigger sperm remain a largely open question. Comparative analyses show positive, negative or no relationship between sperm mass and sperm competition risk (reviewed by Pitnick et al. 2009, Pizzari and Parker 2009), and sperm length varies enormously across taxa. Particularly enigmatic are those insect species in which males produce relatively few, gigantic sperm, as a result – it is presumed - of postcopulatory sexual selection (e.g. Bjork and Pitnick 2006).

Early theoretical models showed that the relationships between sperm size (mass) and number with increasing sperm competition can be complex (Parker 1993). The analyses have involved two trade-off assumptions. In the *direct trade off*, each male has a fixed mass, M, to expend on gametes, and sperm mass and sperm number are traded off directly under the constraint that $M = ms$ (e.g.

Parker et al. 1972, Parker 1982). In the *indirect trade off*, each male has a fixed budget for male reproductive activity, *R*, and energy spent on mate acquisition (mate searching, courtship, fighting for mates, etc.) is traded off against energy spent on ejaculates, so that as ejaculate expenditure increases, the number of matings, *n*, decreases (e.g. Parker 1993). Thus *n*, *s*, and *m* can each be varied independently under the constraint that $R = n(C + Dms)$, where *C* is the energy cost of gaining a mating and *D* is a constant that converts ejaculate expenditure into the same units as *R* and *C*.

Typically, in empirical data, a negative relation between sperm mass and number would be claimed as evidence for a direct size-number trade off. The review of Snook (2005) lists species showing three such cases, though a further eight show no relationship.

While the direct size/number trade off has been used in models of the origin and maintenance of anisogamy (Parker et al. 1972, Parker 1982), it is a misconception that this assumption underpins sperm competition game models devised to explain the relation between ejaculate characteristics such as sperm mass and number in relation to sperm competition level. The latter have all been based on the indirect trade off in which ejaculate expenditure trades off against expenditure on increasing the number of matings. A reason for the use of the direct trade off in early models of anisogamy was that the initial state was anticipated to be a sessile, externally fertilising, marine organism that releases gametes into the sea; the prospects of males searching for mates was not included in this ancestral setting, in which the only reproductive expenditure was gametes.

We here investigate the indirect trade off under three sperm competition mechanisms (Fig. 1): the raffle model (Parker et al. 1990), which appears to approximate to conditions where there is no constraint on the space for fertilisation, such as external fertilising species or many vertebrates with internal fertilisation, and two versions of the direct displacement model (Parker and Simmons 1991), which can apply when females have relatively small sperm stores with a fixed volume such as found in many insects. All three scenarios are analysed using the risk model (Parker 1998), in which a female is assumed to mate once (and hence no sperm competition is involved) with

probability (1-q), and to mate twice with probability q (resulting in sperm competition between just two ejaculates). Thus for each batch of eggs, there are on average (1+q) matings. The model is not appropriate for high levels of sperm competition (intensity models; see Parker 1998, Parker and Pizzari in press) in which typically several ejaculates compete for a given set of eggs.

It should be noted that some sperm competition game models incorporate a distribution of matings (e.g. Williams et al. 2005, Engqvist and Reinhold 2006, Fromhage et al. 2008), which is more realistic but less tractable analytically. Our analysis should be accurate for relatively low risk situations where there are rarely more than two matings per female mating cycle. Also, note that by fixing the probability that a female remates, we are assuming that mating frequency is controlled by females (see Fromhage et al. 2008). This contrasts with models that (implicitly) assume male control of mating frequency (e.g. Williams et al. 2005; see Fromhage et al. 2008), and which may generate different results.

Considerable attention has been paid to the effects of extrinsic loadings in sperm competition 'raffles' – for instance, due to the mating order, the sperm of a male mating second may experience some form of advantage (or disadvantage) relative to that of a male mating first with a female (e.g. Parker 1990). The present analysis does not include an extrinsic loading; our main aim here is to investigate how sperm mass and number may evolve under different sperm competition mechanisms when sperm mass alone exerts a loading in the raffle that determines paternity outcomes. We therefore exclude extrinsic loadings such as mating order effects, and investigate only the effects resulting from the intrinsic loading due to sperm mass. For similar reasons, we have also excluded female influences on paternity outcome (Eberhard, 1996), which could be important in some species (e.g. Evans and Magurran 2001).

2. General results

As in other sperm competition games (see reviews of Parker 1998, Parker and Pizzari in press) we assume the indirect trade off in 2) above, so that fitness *w* is the product of number of matings (*n*) and the average value of each mating (υ) i.e. $w = n\upsilon$. Following Parker (1993) we call the ESS strategy, I = the pair of strategies, s^*, m^*, and assume that mutations occur as unique events affecting only one strategic parameter, so that a change in *s* does not affect *m*, and vice versa. For simplicity, males are assumed to have no information about the sperm competition risk of a given female at the time of mating (this assumption is often violated; see reviews of Parker 1998, Wedell *et al.* 2002, Parker and Pizzari in press), and hence ejaculate the same number of sperm at each mating, all of similar mass. An arbitrary trivial amount of sperm ensures fertility, so that where $s \neq s^*$ is the mutant strategy, the average value of a mating achieved by the mutant is

$$\upsilon(s,\mathrm{I}) = [(1-q) + 2qG(s,\mathrm{I})]/(1+q), \quad (1a)$$

where $G(s,\mathrm{I})$ is the average gain per mating when there is sperm competition, i.e. the average gain achieved (first to mate, second to mate) when the female mates twice.

Where $m \neq m^*$ is the mutant strategy,

$$\upsilon(m,\mathrm{I}) = [(1-q) + 2qG(m,\mathrm{I})]/(1+q), \quad (1b)$$

and the numbers of matings achieved are respectively

$$n(s,\mathrm{I}) = R/(C + Dsm^*), \quad (2a)$$

$$n(m,\mathrm{I}) = R/(C + Ds^*m). \quad (2b)$$

The ESS is defined by

$$\left.\frac{dw(s,\mathrm{I})}{ds}\right|_{s=s^*} = 0, \text{ subject to } \left.\frac{d^2V(s,\mathrm{I})}{ds^2}\right|_{s=s^*} < 0 \quad (3)$$

and similarly for $w(m,\mathrm{I})$ (see Maynard Smith 1982).

Applying technique (3) separately to $w(s,\mathrm{I})$ and $w(m,\mathrm{I})$, and remembering that at the ESS, the expected gain from a mating in which there is sperm competition between two males is G^*=1/2, we obtain

$$m^* = 2qG'(s^*,\mathrm{I})(C + Ds^*m^*)/D, \quad (4a)$$

$$s^* = 2qG'(m^*,\mathrm{I})(C + Ds^*m^*)/D. \qquad (4b)$$

Since at the ESS, the number of matings for females must be consistent with the number for males, we set the ESS matings per male per female cycle as

$$n^* = \frac{N_f}{N_m}(1+q) \qquad (5)$$

where N_f, N_m are the number of breeding females and males respectively (Parker and Ball 2005, Ball and Parker 2007). Thus at the ESS, remembering that

$$n^*(C + Ds^*m^*) = R,$$

$$(C + Ds^*m^*) = RN_m/(1+q)N_f,$$

so that as the probability of double mating, *q*, increases, the cost of acquiring each mating, *C*, decreases. We shall assume throughout an adult sex ratio of unity ($N_f = N_m$), so that

$$(C + Ds^*m^*) = R/(1+q).$$

Hence calling

$$\beta \equiv \left(\frac{R}{D}\right)\left(\frac{2q}{1+q}\right),$$

$$m^* = \beta G'(s^*,\mathrm{I}), \qquad (6a)$$

$$s^* = \beta G'(m^*,\mathrm{I}), \qquad (6b)$$

and we can obtain the relational rule that whatever the sperm competition risk level,

$$s^*G'(s^*,\mathrm{I}) = m^*G'(m^*,\mathrm{I}), \qquad (7)$$

as obtained earlier by Parker (1993) using a slightly different approach. Essentially, rule (7) states that at the ESS, sperm number times the marginal gains through sperm numbers equals sperm mass times the marginal gains through sperm mass. It is anticipated that (7) will apply generally to a wide variety of cases of low sperm competition risk where ejaculate expenditure trades off against number of matings.

3. Models of three mechanisms

The raffle and displacement models represent two extremes of a continuum in sperm competition mechanism (Parker and Pizzari, in press). At one extreme (raffle), fertilisation is external, or sperm occur at very low numbers relative to the volume of the female tract and hence are not constrained by the storage organs of the female (Fig. 1a); they compete numerically for fertilisation in proportion to their input to the tract, as tickets in a raffle (= lottery), in which nevertheless each sperm (ticket) may not be equal (the loaded raffle, Parker and Simmons 1991).

At the other extreme, common in insects (Simmons 2001), the female sperm storage organs are of a fixed volume (often approximately the same order as the volume of ejaculates received) so that, during the input of a second ejaculate, stored sperm are displaced volumetrically (Fig. 1b, c). The sperm displacement model developed by Parker and Simmons (1991) is designed for cases where the female sperm stores have fixed capacity, the incoming ejaculate continuously displaces an equal volume of fluid from the sperm store during input, and there is instant random mixing in the stores. The original model did not include variation in sperm mass. Here we apply this mechanism to two situations. In the first, the sperm are transported in a large volume of seminal fluid so that small changes in sperm mass do not significantly influence displacement (Fig. 1b). In the second, the seminal fluid is small relative to the total mass of sperm in the ejaculate; displacement is mainly due to the sperm themselves and so changes in sperm mass affect the amount of displacement (Fig. 1c). In displacement models, the proportion of offspring gained by a given male depends not only on his ejaculate characteristics, but also on whether he mates first or second with the female.

2.1 Raffle model

We develop the approach of Parker (1993), who assumed that the success of male *i* in competition with male *j* follows the loaded raffle, i.e. $r_i s_i / (r_i s_i + r_j s_j)$, where the sperm numbers ejaculated are by *i* and *j* are s_i, s_j and the competitive values of each sperm in the fertilization raffle are r_i and r_j

respectively. The sperm loading factor, *r*, depends on both the size (mass) and the number of competing sperm: specifically, the 'competitive weight' of a given sperm depends both on its mass *m*, and on the competing sperm density, i.e. the sperm number per unit volume of space available for sperm competition in the arena for fertilisation (e.g. the spermathecae in insects, or the sperm pool surrounding the unfertilised eggs in vertebrates). We thus derive the ESS sperm mass and number making explicit assumptions about the relationship $r_i(m_i,S)$, the competitive loading for a sperm from male *i* that has sperm of mass m_i when the sperm density during competition for fertilizations is proportional to $S = s_i + s_j$.

First consider a mutant male deviating only in sperm numbers, that has the ESS sperm mass, m^*. Thus the competing males both have the same sperm mass (m^*), but the competitive value (loading factor *r*) of the sperm of both the mutant and his competitor are altered equally because the sperm density has changed, i.e. both now have same loading, $r(s,s^*,m^*)=r_s$. Thus a mutant male playing $s \neq s^*$ in a population where all other males play the ESS has a gain under sperm competition of

$$G(s,\mathrm{I}) = r_s s/(r_s s + r_s s^*) = s/(s+s^*), \qquad (8)$$

and differentiating with respect to *s*, we see that at the ESS (where $s = s^*$)

$$G'(s^*,\mathrm{I}) = 1/4s^*, \qquad (9)$$

A mutant playing $m \neq m^*$ has the ESS sperm number, but a competitive loading of $r(s^*,m)$ rather than the ESS $r(s^*,m^*) = r^*$, thus

$$G(m,\mathrm{I}) = r(m,\mathrm{I})/(r(m,\mathrm{I}) + r^*), \qquad (10)$$

and differentiating with respect to *m*, at the ESS (where $m = m^*,\ r = r^*$)

$$G'(m^*,\mathrm{I}) = r'(m^*,\mathrm{I})/4r^*. \qquad (11)$$

It is then easy to obtain

$$m^* s^* = v^* = \frac{R}{2D}\left(\frac{q}{1+q}\right) = \beta/4. \qquad (12)$$

The product of sperm mass and number (which we call v^*) is therefore independent of $r(m,\mathrm{I})$, and increases with sperm competition risk (q) and the resources available for reproduction (R).

Also, from (9) and (11)

$$r'(m,\mathrm{I}) = \frac{r^*}{m^*}, \qquad (13)$$

which is the familiar marginal value theorem solution for sperm mass (see Eq. (10) of Parker, 1993), and shows that (i) an intermediate sperm mass can be achieved only if $r(m,\mathrm{I})$ increases with decreasing gradient (Fig. 2, see also Fig. 1 of Parker, 1993), and (ii) if r is a function only of mass m, sperm mass is optimised independently of sperm competition risk q, so that any dependency of sperm mass on q can be achieved only indirectly through the effects of sperm density (which typically depends on sperm competition risk) on the competitive benefits of sperm mass (see also Parker 1993; 1998; Pizzari and Parker 2009).

2.2 Displacement model 1: displacement mainly by seminal fluid

Here the ejaculate contains sperm at relatively low density in copious seminal fluid, so that small changes in sperm mass exert trivial effects on displacement (Fig. 1b). The female's sperm store can hold a maximum of $S_{\max}$ sperm in their accompanying seminal fluid. Each ejaculate unit input displaces a proportion of α units of fluid from the female's sperm store. Thus if $\alpha = 1$, there is one-for-one output per input as should apply in insects with direct displacement in which the male ejaculates sperm into the spermatheca (the sperm store) itself, as occurs functionally through complex mechanisms, e.g. in the beetle *Aleochara curtula* (Gack and Peschke 1994) and the locust *Locusta migratoria* (Gregory 1965). However, most insects, e.g. the fly *Scatophaga* (= *Scathophaga*) *stercoraria* (Simmons et al. 1999; Hosken and Ward 2000) show indirect displacement in which the sperm are first ejaculated into the bursa or some other part of the female tract, and are later moved to the spermatheca; here typically $\alpha < 1$. Increasing levels of

displacement per unit of ejaculate input can be modelled by increasing $\alpha/S_{\max}$, which acts as a single constant.

From the analysis of Parker and Simmons (1991), we can see that when a mutant male deviating in sperm number (s) competes with an ESS male, the proportion of mutant sperm in the female's sperm store depends whether he mates first or second. When the mutant is second (male 2), his sperm proportion is

$$P_2(s_1^*, s_2) = \left(\frac{1 - e^{-\alpha s_2 / S_{\max}}}{1 - e^{-\alpha (s_2 + s_1^*)/S_{\max})}} \right), \tag{14a}$$

and when he first to mate (male 1), his proportion is

$$P_1(s_1, s_2^*) = 1 - P_2(s_1, s_2^*) = \left(1 - \frac{1 - e^{-\alpha s_2^* / S_{\max}}}{1 - e^{-\alpha (s_1 + s_2^*)/S_{\max})}} \right). \tag{14b}$$

We assume that once displacement has finished, sperm competition follows the rules of the raffle loaded by the relative benefits of sperm mass. Thus for a mutant deviating in sperm number s,

$$G(s,\mathrm{I}) = 0.5 \left(\frac{r_s P_1(s_1, s_2^*)]}{r_s P_1(s_1, s_2^*)] + r_s P_2(s_1, s_2^*)]} + \frac{r_s P_2(s_1^*, s_2)}{r_s P_2(s_1^*, s_2) + r_s P_1(s_1^*, s_2)} \right).$$

Since all sperm have the ESS sperm mass, m^*, the competitive loading, $r_s = r(m^*, s, s^*)$, cancels from the equation because a deviation in sperm number affects the loading r of both males equally. Further, $P_1 + P_2 = 1.0$ in a given female, so

$$G(s,\mathrm{I}) = 0.5 \left(P_1(s_1, s_2^*) + P_2(s_1^*, s_2) \right). \tag{15}$$

In contrast, if a mutant male deviates in sperm mass but not sperm number, since displacement in this model is independent of sperm mass, the proportions of sperm in the sperm stores are unaffected (P_1^* and P_2^* take their ESS values) and so

$$G(m,\mathrm{I}) = 0.5 \left(\frac{r(m,\mathrm{I}) P_1(s_1^*)}{r(m,\mathrm{I}) P_1(s_1^*) + r(m^*,\mathrm{I}) P_2(s_2^*)} + \frac{r(m,\mathrm{I}) P_2(s_2^*)}{r(m,\mathrm{I}) P_2(s_2^*) + r(m^*,\mathrm{I}) P_1(s_1^*)} \right). \tag{16}$$

We therefore obtain at the ESS

$$G'(s,\mathrm{I}) = \frac{\alpha}{2 S_{\max}} \left(\frac{1}{e^{\alpha s^* / S_{\max}} - e^{-\alpha s^* / S_{\max}}} \right). \tag{17}$$

Call $x \equiv \alpha s^* / S_{\max}$; if x is small, $e^x \approx 1+x$, and $e^{-x} \approx 1-x$, so that $1/(e^x - e^{-x}) \approx 1/2x$. Note that the total sperm from a given male that will enter the sperm stores is αs^*. Thus when the total sperm entering the store is tiny relative to the store capacity ($\alpha s^* << S_{\max}$), there is virtually only input of sperm into the sperm stores and no displacement, so that (17) gives $G'(s^*,\mathrm{I}) \approx 1/4s^*$ following (9) for the raffle model, as expected if there is no constraint due to sperm store capacity.

Remembering that $\beta \equiv (R/D)/[2q/(1+q)]$, we obtain from (6a) and (17)

$$m^* = \beta \frac{\alpha}{2S_{\max}} \left(\frac{1}{e^{\alpha s^*/S_{\max}} - e^{-\alpha s^*/S_{\max}}} \right), \qquad (18)$$

and since $P_1^* + P_2^* = 1.0$,

$$G'(m,\mathrm{I}) = \left(P_1^* P_2^*\right) \left(\frac{r'(m,\mathrm{I})}{r^*} \right). \qquad (19)$$

Note that if $P_1^* = P_2^* = 0.5$, we obtain $G'(m,\mathrm{I}) = r'(m,\mathrm{I})/4r^*$ as expected for the raffle; see (11).

2.3. Displacement model 2: displacement mainly by sperm mass

In the previous section, displacement was mediated mainly by seminal fluid. We can modify the analysis to allow displacement to be mediated mainly by sperm mass. Call the fixed volume of the female's sperm stores $V_{\max} \equiv S_{\max}^* m^*$, where $S_{\max}^*$ is now the number of sperm of ESS mass m^* that fill the female's sperm stores. A male inputs volume $v = ms$ sperm mass units into the female tract. Again, (i) each unit input has a probability α of entering the sperm store, and thus (ii) a total volume of $\alpha ms = \alpha v$ incoming units displaces an equal volume from the sperm store continuously during input, and (iii) there is instant random mixing in the sperm stores. Increasing levels of displacement are again modelled by increasing $\alpha / V_{\max}$.

When the mutant is male 2, the 'volumetric proportion' of the sperm stores his sperm occupy is

$$P_2(v_1^*, v_2,) = \left(\frac{1 - e^{-\alpha v_2 / V_{\max}}}{1 - e^{-\alpha (v_2 + v_1^*)/V_{\max})}} \right) \qquad (20a)$$

in which $v_1^* = s_1^* m_1^*$; $v_2 = s_2 m_2^*$ if the mutant deviates in sperm number, or $v_2 = s_2^* m_2$ if it deviates in sperm mass.

When he is male 1, his 'volumetric proportion' is

$$P_1(v_1, v_2^*) = 1 - P_2(v_1, v_2^*) = \left(1 - \frac{1 - e^{-\alpha v_2^* / V_{\max}}}{1 - e^{-\alpha (v_1 + v_2^*)/V_{\max})}}\right) \qquad (20b)$$

in which $v_2^* = s_2^* m_2^*$, and $v_1 = s_1 m_1^*$ if the mutant deviates in sperm number and $v_1 = s_1^* m_1$ if it deviates in sperm mass.

Thus for a mutant deviating in sperm numbers, *s*,

$$G(s,\mathrm{I}) = 0.5\left(r_s P_1(v_1, v_2^*) + r_s P_2(v_1^*, v_2)\right) / \left(r_s (P_1 + P_2)\right) = 0.5\left(P_1(v_1, v_2^*) + P_2(v_1^*, v_2)\right) \qquad (21)$$

c.f. (15).

If the mutant male varies sperm mass but not sperm number,

$$G(m,\mathrm{I}) = 0.5\left(\frac{r(m,\mathrm{I}) P_1(v_1, v_2^*)}{r(m,\mathrm{I}) P_1(v_1, v_2^*) + r^* P_2^*} + \frac{r(m,\mathrm{I}) P_2(v_1^*, v_2)}{r(m,\mathrm{I}) P_2(v_1^*, v_2) + r^* P_1^*}\right) \qquad (22)$$

c.f. (19), where again r^*, P_1^* and P_2^* are the ESS values.

We therefore obtain at the ESS

$$G'(s,\mathrm{I}) = \frac{\alpha m^*}{2V_{\max}}\left(\frac{1}{e^{\alpha v^* / V_{\max}} - e^{-\alpha v^* / V_{\max}}}\right). \qquad (23)$$

Applying the general equation (6a) we get

$$e^{\alpha v^* / V_{\max}} - e^{-\alpha v^* / V_{\max}} = \frac{\alpha R}{V_{\max} D}\left(\frac{q}{1+q}\right). \qquad (24)$$

Note that v^* is independent of the competitive benefits of sperm mass, $r(m, s^*)$, and depends solely on, and increases with, the combined constant on the right hand side. Here, $\alpha R / D V_{\max}$ could be called the 'capacity for displacement', and is equivalent to δ of Charnov (1996), i.e. the male's sperm production potential divided by the female's sperm storage volume; $q/(1+q)$ relates to risk and increases with *q*. Though an explicit solution for ESS ejaculate mass, v^*, cannot be obtained from (24), v^* can readily be solved numerically.

Remembering that $P_1^* + P_2^* = 1.0$,

$$G'(m,\mathrm{I}) = \left\{ \left(P_1^* P_2^*\right) \frac{r'(m,\mathrm{I})}{r^*} + \frac{1}{2}\left(P_1'(m,\mathrm{I}) P_2^* + P_2'(m,\mathrm{I}) P_1^* \right) \right\}, \tag{25}$$

which is similar to (19); the additional term on the right hand side arises because sperm mass also has an effect on displacement.

We can show that

$$P_1'(m,\mathrm{I}) = \frac{\alpha s^*}{V_{\max}} \left(\frac{e^{-2\alpha v^*/V_{\max}} \left(1 - e^{-\alpha v^*/V_{\max}}\right)}{\left(1 - e^{-2\alpha v^*/V_{\max}}\right)^2} \right), \text{ and} \tag{26}$$

$$P_2'(m,\mathrm{I}) = \frac{\alpha s^*}{V_{\max}} \left(\frac{e^{-\alpha v^*/V_{\max}} \left(1 - e^{-\alpha v^*/V_{\max}}\right)}{\left(1 - e^{-2\alpha v^*/V_{\max}}\right)^2} \right), \tag{27}$$

so that (25) becomes

$$G'(m,\mathrm{I}) = \frac{r'(m,\mathrm{I})}{r^*} \left(\frac{e^{-\alpha v^*/V_{\max}} \left(1 - e^{-\alpha v^*/V_{\max}}\right)^2}{\left(1 - e^{-2\alpha v^*/V_{\max}}\right)^2} \right) + \frac{\alpha s^*}{V_{\max}} \left(\frac{2e^{-2\alpha v^*/V_{\max}} \left(1 - e^{-\alpha v^*/V_{\max}}\right)^2}{\left(1 - e^{-2\alpha v^*/V_{\max}}\right)^3} \right). \tag{28}$$

Thus inserting (23) and (28) into the general equation (7), we obtain

$$\frac{r'(m,\mathrm{I})}{r^*} = \frac{\alpha s^*}{V_{\max}} A, \tag{29a}$$

where $A = \left[\frac{\left(1 - e^{-2\alpha v^*/V_{\max}}\right)}{\left(1 - e^{-\alpha v^*/V_{\max}}\right)^2} - \frac{2e^{-\alpha v^*/V_{\max}}}{\left(1 - e^{-2\alpha v^*/V_{\max}}\right)} \right]$. (29b)

3. How can sperm numbers affect the competitive advantage of sperm mass, $r(m,\mathrm{I})$?

The function $r(m,\mathrm{I})$ defines how sperm mass affects fertilisation success. To obtain an intermediate optimum for sperm mass (m^*) in the raffle model, $r(m,\mathrm{I})$ must satisfy the marginal value theorem requirement that a tangent can be drawn from the origin (see equation (13) and Fig. 2), and m^* can alter with sperm competition risk q only if the form of $r(m,\mathrm{I})$ changes with q (see

also Parker 1993). We later show that these features also apply to the displacement models. The most obvious way for such a dependency to occur would be through a dependency between $r(m,\mathrm{I})$ and sperm density, which we know to be related to sperm competition risk, q (e.g. see equations (12) and (24)).

We base our further analyses on three versions of $r(m,\mathrm{I})$ that obey exponentially diminishing returns and allow a tangent to be drawn from the origin:

$$r(m,\mathrm{I}) = f_1\left(1 - e^{-(m-m_{\min})}\right), \tag{30a}$$

$$r(m,\mathrm{I}) = \left(1 - e^{-f_2(m-m_{\min})}\right), \tag{30b}$$

$$r(m,\mathrm{I}) = \left(1 - e^{-(m-f_3 m_{\min})}\right). \tag{30c}$$

The effect of sperm density on the competitive weight due to sperm mass is included as the 'sperm density' function $f(s^*)$, i.e. f_1, f_2, f_3, depending on the version of $r(m,\mathrm{I})$ above. Thus each $f(s^*)$ function, which may either increase or decrease with sperm numbers, exerts a different effect on the form of $r(m,\mathrm{I})$ (see Fig. 2): f_1 changes the asymptotic value, f_2 changes the rate at which r rises to its asymptote, and f_3 changes the intercept value ($m_0 = f_3 m_{\min}$ the minimum sperm mass to have an r value exceeding zero). Fig. 2 shows how unilateral changes in f_1, f_2, f_3 affect the marginal value result for sperm mass, m^*, in the raffle model. Changes in the asymptote (through changes in function f_1) will not affect ESS sperm mass (Fig. 2a; see Section 5.1). Increasing the rate of approach to the asymptote (by increasing f_2) *decreases* the ESS sperm mass (Fig. 2b; see Section 5.2), and increasing the minimum sperm mass, m_0 (by increasing f_2) *increases* the ESS sperm mass (Fig. 2c; see Section 5.3).

We next examine the effects of each of sperm density function, f_1, f_2, f_3, separately for each of the three sperm competition models, to examine how they may affect (i) the ESS total ejaculate mass ($v^* = m^* s^*$), (ii) ESS sperm mass (m^*) and sperm number (s^*), and (iii) the relationship between sperm mass and number within the total ejaculate mass (m^*/s^*). To do this, we use explicit versions of $f(s^*) = f_1, f_2, f_3$ for each sperm competition model.

For the raffle model, the total sperm in competition, $S = 2s^*$. Thus for the case where increasing sperm density increases f we use

$$f_{Rinc}(s^*) = \left(2bs^*\right)^u, \tag{31a}$$

and for the case where increasing sperm density decreases f

$$f_{Rdec}(s^*) = \left(2bs^*\right)^{-u}, \tag{31b}$$

where b and u are constants.

After displacement in displacement model 1, the sperm number in the sperm stores is $S_{\max}(1-e^{-2\alpha s^*/S_{\max}})$, and so by analogy we use

$$f_{D1inc}(s^*) = \left(bS_{\max}(1-e^{-2\alpha s^*/S_{\max}})\right)^u, \tag{32a}$$

$$f_{D1dec}(s^*) = \left(bS_{\max}(1-e^{-2\alpha s^*/S_{\max}})\right)^{-u}. \tag{32b}$$

After displacement in displacement model 2, the total sperm mass in the stores is $V_{\max}(1-e^{-2\alpha v^*/V_{\max}})$, and so we use f functions related to v

$$f_{D2inc}(v^*) = \left(bV_{\max}(1-e^{-2\alpha v^*/V_{\max}})\right)^u, \tag{33a}$$

$$f_{D2dec}(v^*) = \left(bV_{\max}(1-e^{-2\alpha v^*/V_{\max}})\right)^{-u}. \tag{33b}$$

All three sperm competition models include $r(m,\mathrm{I})$ only as the term $r'(m,\mathrm{I})/r(m,\mathrm{I})$; see equations (13), (19), (25). Note that in the raffle and displacement model 1, the competition terms ($f_{Rinc}, f_{Rdec}, f_{D1inc}, f_{D1dec}$) are functions only of s, so that they act as constants in $r(m,\mathrm{I})$. In displacement model 2, the competition terms (f_{D2inc}, f_{D2dec}) are functions of both s and m. Increasing the exponent u above 1.0 in the sperm density functions causes increasing deviations in $r(m,\mathrm{I})$ as sperm density increases.

4. Procedures for obtaining results

For most of the cases analysed, we were unable to derive explicit solutions for m^* and s^*, but numerical values across a wide range of q (usually from 0.02 to 0.98) could be obtained by iterative procedures using the equations given in the following sections. Iterations calculated Δ (= right hand minus left hand side of the equation), and then changed m or s until $\Delta = 0$, giving the ESS variable value (m^* or s^*). To check the validity of the values obtained, Δ was calculated at given q for increasing values of the variable (e.g. from $m_{\min}$ or m_0 to some high m value) to ensure that there was only one solution (typically, when $\Delta = 0$ twice across the range investigated, one solution could be logically discarded, e.g. $m^* < m_{\min}$ or m_0). Finally, candidate ESSs (I = m^*, s^*) were tested for local stability by calculating the fitness ($w = n\upsilon$) of a mutant deviating unilaterally from m^* or s^*. Mutant values for υ are specified in equations (1a), (1b); mutant n values were calculated as follows. In a population at the ESS the costs of acquiring a mating (C) are constant and specified by the constraint equation $n^*(C + Ds^*m^*) = R$. With a unity sex ratio $n^* = (1+q)$, hence $C = R/(1+q) - Ds^*m^*$. A mutant deviating as $m \neq m^*$, gets $n = R/(C + Ds^*m)$ matings, and substituting C we obtain

$$n(m,\mathrm{I}) = \frac{R(1+q)}{R + Ds^*(1+q)(m-m^*)}.$$

A parallel equation is obtained for $n(s,\mathrm{I})$ for mutants deviating as $s \neq s^*$.

In Figs 3 to 5 we examine the responses of the ESS sperm mass and number (m^*, s^*) to changes in sperm competition risk (q) at the same set of default values for the parameters for each panel of figures. We also examined the effect of unilateral increases in each of the other parameters from these default values; results of this procedure for the q range 0.02 to 0.98 are summarised in Tables 1 to 3.

5. Results for the raffle model

5.1. Sperm numbers change the asymptotic value of $r(m,\mathrm{I})$

For the raffle and displacement model 1, equation (30a) can be rewritten generally as $r(m,\mathrm{I}) = f_1(s^*)g(m)$. Thus $r'(m,\mathrm{I})/r(m,\mathrm{I}) = g'(m)/g(m)$. The function $f_1(s^*)$, which is the effect of sperm density on the asymptotic value of $r(m,\mathrm{I})$, does not contain the term m; it therefore cancels and is not involved in the optimisation of sperm mass, m^*. Thus the ESS value of m^* in these two models is unaffected if sperm number changes only the asymptote of $r(m,\mathrm{I})$ (Fig. 2a).

Since total sperm mass (i.e. $v^* = m^* s^*$) increases with sperm competition risk, q (see (12)), then if m^* remains constant, the ratio m^*/s^* will decrease with q. This conclusion applies generally if $r'(m,\mathrm{I})/r(m,\mathrm{I})$ is independent of s as in the present case, and more simply when $r(m)$ is independent of s (see Parker 1993).

5.2. Sperm numbers change the rate of approach of $r(m,\mathrm{I})$ to its asymptote

The function $f_2(s^*)$ in equation (30b) models the effect of sperm numbers on the rate at which $r(m,\mathrm{I})$ rises to its asymptote. Then

$$\frac{r'(m,\mathrm{I})}{r(m,\mathrm{I})} = \frac{f_2(s^*)e^{-f_2(s^*)(m-m_{\min})}}{1-e^{-f_2(s^*)(m-m_{\min})}}. \qquad (34)$$

Hence from (13) we obtain

$$m^* = \left(\ln(f_2 m^* + 1)\right)/f_2 + m_{\min}, \qquad (35)$$

and substituting $s^* = \beta/4m^*$ (see (12)) into $f_2 = f_{Rinc}, f_{Rdec}$ in (31a), (31b) we obtain (34) in terms of m^*, which can be then solved numerically (an analytical solution is possible when $u = 1$ in f_{Rinc}).

Some numerical results for sperm mass and number in relation to sperm competition risk in the raffle model are shown in Fig. 3a for the case where increasing sperm numbers *increase* the rate at which r rises to its asymptote, using (31a), and Fig. 3b for the case where increasing sperm numbers *decrease* the rate at which r rises to its asymptote, using (31b). Note that the product, $m^* s^*$, remains the same (= $\beta/4$, see (12)) for both cases, and is set by extrinsic factors of risk (q) and resource availability (R/D) in the term β. Thus at a given β, there is effectively a direct trade off

between size (mass) and number. However, the allocation of m^*, s^* in response to increases in sperm competition differs notably in the two cases. If sperm numbers increase the gradient of r, m^* decreases and s^* increases monotonically with q (Fig. 3a). If sperm numbers decrease the gradient of r, both m^* and s^* increase monotonically with q (Fig. 3b), and in all cases examined, with s^* increasing more rapidly. Thus ESS sperm number appears to increase with risk q, though sperm mass varies in its response to risk, depending on the effect of sperm density on r. The mass/number ratio, m^*/s^*, declined with q under both forms for f_2 (f_{Rinc}, f_{Rdec}) (Fig. 3c) at $u = 1$, but using sperm density function f_{Rdec} with sufficiently high u, m^*/s^* increases with q (see the curve for $u = 10$, Fig. 3c). Thus extreme competitive effects of sperm density can generate a more rapid rise in sperm mass than in sperm number with q.

Experiments in which the other parameters (b, $m_{\min}$, u, R/D) are altered unilaterally from the default values used for Fig. 3 showed that although the absolute magnitudes of m^*, s^* alter, the qualitative relations between m^*, s^* and q remain similar over wide ranges (Table 1a). With sperm density function f_{Rinc} (which increases the slope of r), increasing u decreases s^* at low q and increases s^* at high q, with opposite effects on m^* (at high q and u, $m^* \to m_{\min}$). Increasing $m_{\min}$ increases m^* and decreases s^* at all q. Increasing b and R/D increase s^* and decrease m^*; the product s^*m^* increases in direct proportion to R/D. Using sperm density function f_{Rdec} (which decreases the slope of r) reverses some of these effects. Thus increasing u now increases s^* at low q and decreases s^* at high q, with the opposite effect on m^*. Increasing b now decreases s^* and increases m^*, and increasing R/D increases both s^* and m^*. Increasing $m_{\min}$ increases m^* and decreases s^* at all q, as with f_{Rinc}.

However, in all such experiments, at $u = 1$ the ratio m^*/s^* was always found to be decreasing as in Fig. 3d, and the qualitative relations between m^*, s^*, and q remained unchanged.

Note that in the raffle, with unconstrained space for sperm mixing (Fig. 1a), the expected proportion of offspring sired by each of N competing males is $1/N$; thus in our present model the expected proportion of offspring fertilised by the second of two males (P_2) is always 0.5.

5.3. Sperm numbers change the minimum competitive sperm mass

The function $f_3(s^*)$ in equation (30c) models the effect of sperm numbers on the minimum sperm mass. Then

$$\frac{r'(m,\mathrm{I})}{r(m,\mathrm{I})} = \frac{e^{-(m-f_3(s^*)m_{\min})}}{1-e^{-(m-f_3(s^*)m_{\min})}}. \qquad (36)$$

Hence from (13) we obtain

$$m^* = \left(\ln(m^*+1)\right) + f_3 m_{\min}, \qquad (37)$$

and substituting $s^* = \beta/4m^*$ as before we obtain (37) in terms of m^* alone, which can be then solved numerically.

Numerical results are shown in Fig. 3d for the case where sperm numbers increase the minimum sperm mass ($m_0 = f_3 m_{\min}$), using (31a), and Fig. 3e for the case where increasing sperm numbers decrease the minimum sperm mass ($m_0 = f_3 m_{\min}$), as in (31b). The product, $m^* s^*$, remains unchanged (and equal to Figs. 3a to 3c) because of the direct size/number trade off at a given β. Again, allocation of m^* and s^* in response to sperm competition differs in the two cases. If sperm numbers increase m_0 (Fig. 3d), both m^* and s^* increase monotonically with q. When the effect of sperm density on sperm mass is only moderate or weak (see curve for u = 1, Fig. 3d), s^* increases with q faster than m^*, as under f_2 effects (Figs. 3a, 3b). However, if the sperm density effect is made sufficiently severe by increasing u in f_{Rinc}, m^* increases at a faster rate than s^* (see curve for u = 10, Fig. 3d). If sperm numbers decrease m_0 (Fig. 3e), s^* typically increases steeply with q, while m^* decreases rapidly to m_0 at high q. Thus again, sperm numbers appear always to increase

with sperm competition risk, though sperm mass varies in its response to risk, depending on the effect of f_3 on *r*. The mass/number ratio, m^*/s^* (Fig. 3f), declined with *q* under f_{Rdec} and moderate or weak sperm density effects under f_{Rinc} (at $u = 1$), and as in the previous model for f_2 effects, m^*/s^* could be made to increase with high sperm density effects, but now under f_{Rinc} (see curve for $u = 10$, Fig. 3f).

Experiments varying the other parameters (b, $m_{\min}$, u, R/D) unilaterally from the default values used for Fig. 3 are summarised in Table 1b. If minimum sperm mass increases with sperm density (f_{Rinc}), increasing *u* increases s^* at low *q* and decreases s^* at high *q*, with the opposite effect on m^*, thus m^*/s^* is decreasing with *q* at low *u*, but increasing with *q* at high *u* (Fig. 3f). If minimum sperm mass decreases with sperm density (f_{Rdec}), increasing *u* appears to decrease m^* (bounded by m_0) and to increase s^*; m^*/s^* is thus decreasing with *q*. Increasing $m_{\min}$ and *R/D* have the same qualitative effects as for the function f_2 under both f_{Rinc} and f_{Rdec}, except that with *R/D*, the effects on sperm mass are reversed. Increasing *b* increases m^* and m^*/s^*, and decreases s^* under f_{Rinc}; all these effects reverse under f_{Rdec}.

6. Results for Displacement model 1

6.1. Sperm numbers change the asymptotic value of $r(m,\mathrm{I})$

If sperm density changes the asymptotic value of $r(m,\mathrm{I})$, the value of m^* is unchanged, as with the raffle model, (Fig. 2a). Since the total sperm mass, $v^* = m^* s^*$, increases with *q*, v^* increases solely through increases in s^*. Hence m^*/s^* always decreases with *q* using the sperm density function f_3.

6.2. Sperm numbers change the rate of approach of $r(m,\mathrm{I})$ *to its asymptote*

Using $f_2(s^*)$ in equation (30b) to model the effect of sperm numbers on the rate at which $r(m,\mathrm{I})$ rises to its asymptote, $r'(m,\mathrm{I})/r(m,\mathrm{I})$ follows (34), and with (19) we substitute into general equation (6b) to obtain

$$s^* = \beta\left(P_1^* P_2^*\right)\left(\frac{f_2(s^*)e^{-f_2(s^*)(m-m_{\min})}}{1-e^{-f_2(s^*)(m-m_{\min})}}\right), \qquad (38)$$

where P_1^*, P_2^*, follow (14a), (14b). Thus s^* can be iterated substituting m^* from (18).

Numerical results are shown in Fig. 4a for the case where increasing sperm numbers *increase* the rate at which *r* rises to its asymptote, using (32a), and Fig. 4b for the case where increasing sperm numbers *decrease* the rate at which *r* rises to its asymptote, using (32b). Default values used are $\alpha = 1$ and $S_{\max} = 100$, which give a relatively low capacity for displacement, so that solutions are similar to the raffle (Fig. 3). Thus m^* decreases with *q* if sperm numbers *increase* the slope of *r* (Fig. 4a) and increases with *q* if sperm numbers *decrease* the slope of *r* (Fig. 4b), while s^* increases with *q* in both cases. However, although total ejaculate investment ($v^* = m^* s^*$) again always increases with *q*, and is very similar to the raffle at low displacement, it is strongly reduced as the capacity for displacement ($\alpha/S_{\max}$) increases (shown in Figs. 4a, 4b). Thus at high $\alpha/S_{\max}$, v^* approaches its asymptote quickly with *q*, and becomes almost invariant across higher risk levels. The sperm mass/number ratio decreases with risk *q* (Fig. 4c) for both sperm density functions (f_{D1inc}, f_{D1dec}) at $u = 1$, but as with the raffle, extreme competitive effects ($u = 10$ with f_{D1dec}) generates a positive relation between m^*/s^* and *q*.

Experiments increasing other parameters (b, $m_{\min}$, u, R/D, $\alpha/S_{\max}$) unilaterally from their default values used for Fig. 4 are summarised in Table 2a. The qualitative relations between m^*, s^* and *q* again appear to remain similar over wide ranges. Results are very similar to the raffle (c.f. Table 1a). Thus with sperm density function f_{D1inc} (which increases the slope of *r*), increasing *u* decreases s^* at low *q* and increases s^* at high *q*, with the opposite effect on m^* (at high *q* and *u*, $m^* \to m_{\min}$); reversed effects occur with function f_{D1dec} (which decreases the slope of *r*). Increasing

parameters b, $m_{\min}$ and R/D unilaterally all have similar quantitative effects to the raffle, and at low displacement ($\alpha/S_{\max}$ = 1/100) the total ejaculate mass is almost constant and equal to that for the raffle. The paternity of the second male to mate (P_2) in this model always exceeds 0.5; P_2 increases with q and R/D, and decreases with $m_{\min}$. Its response varies with q under both f_{D1inc} and f_{D1dec}.

6.3. Sperm numbers change the minimum competitive sperm mass

Using $f_3(s^*)$ in (30c) to model sperm numbers changing the minimum sperm mass ($m_0 = f_3 m_{\min}$), $r'(m,\mathrm{I})/r(m,\mathrm{I})$ follows (36), and from (19) and (6b)

$$s^* = \beta\left(P_1^* P_2^*\right)\left(\frac{e^{-(m-f_3(s^*)m_{\min})}}{1-e^{-(m-f_3(s^*)m_{\min})}}\right), \qquad (39)$$

where P_1^*, P_2^*, follow (14a), (14b) and s^* is iterated substituting m^* from (18).

Numerical results using the default parameter values given in Fig. 4 are shown in Fig. 4d for the case where increasing sperm numbers increase minimum sperm mass (32a), and Fig. 4e for the case where increasing sperm numbers decrease the minimum sperm mass (32b). The total ejaculate mass, v^* reduces as $\alpha/S_{\max}$ increases, as with sperm density function f_2. Responses of m^* and s^* to sperm competition risk are generally similar to those for the raffle (c.f. Figs. 3d, 3e, 3f), as might be expected. Again, m^*/s^* typically decreases monotonically with q if the effect of sperm density on sperm mass is moderate or weak (see f_{D1inc}, f_{D1dec} curves for u = 1, Fig. 4f), but as with the raffle, if competitive effects using f_{D1inc} increase severely enough with sperm density they can generate increases in m^*/s^* with q (see curve for f_{D1inc}, u = 10, Fig. 4f). However, under f_{D1dec}, an unusual response was found at $q > 0.72$. The ESS appeared to shift suddenly to lower sperm mass (from m^* = 0.044 to 0.0028) and higher number (from s^* = 46.37 to 271.6). Changes then remained continuous as q increased to its maximum level (across the grey shaded area in Fig. 4e),

with sperm mass decreasing (to 0.0025) and sperm number increasing (to 296.5; not shown in the figure).

Effects of varying the other parameters (b, $m_{\min}$, u, R/D, $\alpha/S_{\max}$) unilaterally from the default values used for Fig. 4 are summarised in Table 2b. Results for b, $m_{\min}$, u, and R/D are again similar to the raffle (c.f. Table 1b), except that the effects of increasing u were variable with q under f_{D1dec} as well as with f_{D1inc} and sperm mass dropped to $m_{\min}$ more quickly with increases in u. At low displacement ($\alpha/S_{\max}$ = 1/100), v^* is almost constant and equal to that for the raffle, but decreases with $\alpha/S_{\max}$. The response of P_2 to q, u, $\alpha/S_{\max}$, $m_{\min}$ and R/D under f_3 is similar to the responses to f_2, but for parameter b the response is reversed.

Thus although structurally very different, displacement mainly by seminal fluid (displacement model 1) generates qualitatively very similar results to the raffle, the main difference being that there is increasing economy in ejaculate investment (v^*) as the capacity for displacement ($\alpha/S_{\max}$) increases.

7. Results for Displacement model 2

Calculations of $r'(m,\mathrm{I})/r(m,\mathrm{I})$ for this model are more complex than the previous models because the sperm density functions in (33a), (33b) are a function of both s and m. To simplify the notation, we set $f_{D2inc} \equiv Z^u$, $f_{D2dec} \equiv Z^{-u}$, where $Z \equiv bV_{\max}(1-e^{-2\alpha s^* m/V_{\max}})$ in (33a), (33b). Since v^*, and hence also P_2, are fixed by extrinsic parameters that are independent of m^* and s^* (see (24)), we first iterate v^*, and then iterate m^* from equations in m^* and v^*.

7.1. Sperm numbers change the asymptotic value of $r(m,\mathrm{I})$

Unlike the raffle and displacement model 1, when sperm density changes the asymptotic value of $r(m,\mathrm{I})$ in this model, m^* changes with q. Using (29a) we get

$$\frac{r'(m,\mathrm{I})}{r(m,\mathrm{I})} = \frac{f_1'(m)}{f_1(m)} + \frac{e^{-(m-m_{\min})}}{1-e^{-(m-m_{\min})}} = \frac{\alpha s^*}{V_{\max}} A. \qquad (40)$$

If sperm mass increases f_1 in (40), we use f_{D2inc} to obtain the result that

$$\frac{m^* e^{-(m^*-m_{\min})}}{1-e^{-(m^*-m_{\min})}} = \left(\alpha v^* A - \frac{2u\alpha v^* e^{-2\alpha v^*/V_{\max}}}{(1-e^{-2\alpha v^*/V_{\max}})} \right) / V_{\max}, \qquad (41)$$

and if sperm mass decreases f_1, applying f_{D2dec} simply changes the sign of u in (41). Note that the solutions for m^* and s^* are independent of parameter *b*.

Default values (α = 1 and $V_{\max}$ = 100) for Fig. 5 again give a relatively low capacity for displacement so that the three models can be compared. For u = 1, using (33a) to model the case where increasing sperm mass *increases* asymptotic *r* shows that m^* increases weakly with *q* (Fig. 5a), and using (33b) to model the case where increasing sperm mass *decreases* asymptotic *r* shows that m^* decreases with *q* (Fig. 5b), though at low *q* values solutions could not be iterated, suggesting an ESS at the limit of maximum sperm mass and minimal numbers. As usual, s^* increases with *q* in both cases. Thus the sperm mass/number ratio, m^*/s^*, declines in both cases (Fig. 5c) at u = 1, as with previous models. This was always found to be the case with f_{D2inc} for u > 1. With f_{D2dec} we were unable to obtain increasing m^*/s^* with *q* for u > 1, though at low *q* huge sperm masses were generated for a wide range of *q* (the grey area in Fig. 5b) and this 'maximum sperm mass' zone increased as u increased. The increase in total ejaculate investment ($v^* = m^* s^*$) with *q* is the same throughout Fig. 5 (as expected from (24)); it is again reduced as the capacity for displacement ($\alpha/V_{\max}$) increases, though less strongly than with displacement by seminal fluid (model 1).

Effects of increasing other parameters (b, $m_{\min}$, u, R/D, $\alpha/V_{\max}$) unilaterally from their default values used for Fig. 5 are shown in Table 3a. With sperm density function f_{D2inc}, increasing u appeared to decrease m^* and m^*/s^*, and increase s^*; the reverse effects occurred with the sperm density function f_{D2dec}. Under f_{D2inc}, increasing the displacement capacity ($\alpha/V_{\max}$) decreased s^* and had a variable effect on m^* and m^*/s^* depending on *q*, but under f_{D2dec}, s^* increased and

m^*/s^* decreased. As with displacement model 1, m^*s^* decreased and P_2 increased with $\alpha/V_{\max}$. Effects of increasing $m_{\min}$ are as in other models, except that P_2 remained constant. Effects of increasing R/D unilaterally are also similar to other models, but note that here m^* increased under f_{D2inc} and decreased under f_{D2dec}.

7.2. Sperm numbers change the rate of approach of $r(m,\mathrm{I})$ *to its asymptote*

From (29a) we get

$$\frac{r'(m,\mathrm{I})}{r(m,\mathrm{I})}=\frac{\left[f_2'(m)(m-m_{\min})+f_2(m)\right]e^{-(m-m_{\min})}}{1-e^{-(m-m_{\min})}}=\frac{\alpha s^*}{V_{\max}}A. \qquad (42)$$

If sperm mass increases f_2, using f_{D2inc} in (42) gives

$$m-m_{\min}=\left(\frac{Z}{2ub\alpha v^* e^{-2\alpha v^*/V_{\max}}}\right)\left(\frac{\alpha v^* A}{Z^u V_{\max}}\left(\frac{e^{-(m^*-m_{\min})}}{1-e^{-(m^*-m_{\min})}}\right)-m\right), \qquad (43)$$

and if sperm mass decreases f_2, using f_{D2dec} again simply changes the sign of *u*.

Results for this case (Figs. 5d, 5e, 5f) should be compared with those for the raffle (Figs. 3a, 3b, 3c) and displacement model 1 (Figs. 4a, 4b, 4c). Qualitative effects remain as before, i.e. where increasing sperm numbers *increase* slope of *r* (function (33a)), m^* decreases and s^* increases with *q*, and these relations are reversed when increasing sperm numbers *decrease* slope of *r* (function (33b)). However, the present model generates rather different relations quantitatively, e.g. notably reducing the increase in sperm mass with *q* under f_{D2dec} (Fig. 5e). As in other models, at $u = 1$, m^*/s^* decreases with *q* (Fig. 5f). We were again unable to generate an increasing relation between m^*/s^* with *q* by increasing $u > 1$ in either f_{D2inc} or f_{D2dec}.

Effects of increasing the other parameters (b, $m_{\min}$, u, R/D, $\alpha/V_{\max}$) unilaterally from their default values are shown in Table 3b. As with the other sperm competition mechanisms, increasing *u* under f_{D2inc} tended to show m^*, s^* responses varying with *q*, but under f_{D2dec} we obtained only

increasing m^* and decreasing s^* across q {0.02, 0.098}. Variable responses (but often almost invariant) of m^* and s^* also occurred with increases in $\alpha/V_{\max}$, though s^* decreased under f_{D2dec}. As before P_2 always increased with $\alpha/V_{\max}$. Responses to b, $m_{\min}$ and R/D were the same as for displacement model 1, except that in the present model P_2 remained constant with b and $m_{\min}$.

7.3. Sperm numbers change the minimum competitive sperm mass

Using (29a) we get

$$\frac{r'(m,\mathrm{I})}{r(m,\mathrm{I})}=\frac{\left[1-m_{\min}f_3'(m)\right]e^{-(m-f_3m_{\min})}}{1-e^{-(m-f_3m_{\min})}}=\frac{\alpha s^*}{V_{\max}}A. \qquad (44)$$

If sperm mass increases f_3, applying f_{D2inc} in (40) gives the result that

$$m=\frac{\alpha v^* A}{V_{\max}}\left(\frac{e^{-(m^*-f_3m_{\min})}}{1-e^{-(m^*-f_3m_{\min})}}\right)+m_{\min}2ub\alpha v^* e^{-2\alpha v^*/V_{\max}}Z^{u-1}, \qquad (45)$$

and if sperm mass decreases f_3, using f_{D2dec} again changes the sign of u.

Results for this model are shown in Fig. 5g, 5h, 5i, and give the greatest differences from previous results (note difference scales to the y axes). Under f_{D2inc}, s^* is high and almost invariant across q, and the increase in v^* is due to increases in m^* (Fig. 5g). Under f_{D2dec}, s^* increases and m^* decreases steeply with q (Fig. 5h), generating the typical declining m^*/s^* response (Fig. 5i). Unusually, m^*/s^* increases under f_{D2inc} even at u = 1, an effect generated in no other model.

Effects of increasing the other parameters (b, $m_{\min}$, u, R/D, $\alpha/V_{\max}$) unilaterally from their default values are shown in Table 3c. We could not obtain solutions for more than extremely small increases in u =1, so predictions here must be regarded with caution. Under f_{D2inc}, increases in displacement capacity ($\alpha/V_{\max}$) generated variable sperm mass and number responses that varied with q, but under f_{D2dec} responses were similar to model 1. Responses to b, $m_{\min}$ and R/D were

again the same as for model 1, except that in the present model P_2 remained constant with b and $m_{\min}$.

8. The relation between P_2 and q

Our models include only the loading in the fertilisation raffle that is generated by sperm mass differences between males. Thus in the raffle $P_2 = 0.5$, and in the displacement models $P_2 > 0.5$, and increasing with q.

Fig. 6 shows the relation between P_2 and sperm competition risk q generated under displacement models 1 and 2. In all variants of both models, P_2 rises with risk, q, from a minimum of 0.5 as $q \to 0$. Both increased resource level (R/D) and increased sperm displacement capacity ($\alpha/S_{\max}$ in model 1; $\alpha/V_{\max}$ in model 2) increase P_2. We show two levels of displacement capacity (low and high) in Fig. 6. With displacement model 1, when sperm density changes the slope of $r(m)$ (sperm density function f_2), at low displacement capacities P_2 rises more quickly under f_{D1inc} than under f_{D1dec}; the reverse is the case with high displacement capacity (Fig. 6a). When sperm density changes the minimum sperm mass (sperm density function f_3), at low to moderate q levels f_{D1inc} and f_{D1dec} exert the opposite effects: at low displacement capacities P_2 increases less quickly under f_{D1inc} than under f_{D1dec}; the reverse is the case with high displacement capacity (Fig. 6b). At high q levels the discontinuity in sperm mass generated under $f_3 = f_{D1dec}$ (Fig. 4e) causes an abrupt discontinuity in P_2 just at $q = 0.726$; the increase in sperm number above this q level causes P_2 to rise to that of the high displacement capacity.

With displacement model 2 (Fig. 6c), all variants of the model have the same P_2 at a given q, $\alpha/V_{\max}$, and R/D level, set by (24), which determines v^*. The asymptotic P_2 (at high q) is lower than that for model 1.

9. Discussion

9.1. Summary of results

We stress that our models relate to low sperm competition risk; at high risk or intensity levels conclusions are likely to be different (see Introduction). The present analysis confirms some of the previous results (Parker 1993) for the risk model. Function $r(m)$, the fertilization competitiveness of a sperm in relation to its mass, must have a form such that a marginal value theorem tangent can be drawn from the origin; i.e. it must either be sigmoidal, or increasing with decreasing gradient from a positive intercept (as in Fig. 2), otherwise the ESS sperm mass is at the minimum or maximum limit. Changes in sperm mass with sperm competition level can arise only when $r(m)$ changes with sperm competition level. The most obvious mechanism for such dependency is where $r(m)$ depends on the sperm density in the female tract (see also Parker 1993). In the present analysis, setting $u = 0$ in the sperm density functions in equations (31a) to (33b) removes this dependency, and results in the same ESS sperm mass at all risk levels.

In all our models, sperm numbers (s^*) and total ejaculate mass ($v^* = m^* s^*$) rise continuously with risk q (see also Parker and Ball 2005). In the raffle model, v^* is constant at given values of q and R/D (12), and in displacement model 2 (displacement by sperm mass) v^* is constant at given values of q and $\alpha R/DV_{\max}$. In these models, v^* is independent of $r(m)$, and is increased by risk q, resource levels, R/D, and (for displacement model 2) capacity for displacement $\alpha/V_{\max}$. Displacement model 1 (displacement by seminal fluid) is almost invariant with parameters in $r(m)$, and hence shows similar properties. Thus at a given risk, resources and displacement capacity level, sperm size (mass) and number effectively trade off directly against each other. This finding has important implications for empiricists examining evidence for size-number trade offs (see Section 9.2).

Though v^* is invariant at a given sperm competition level q, the allocation within v^* to sperm mass (m^*) and number (s^*) is complex, and depends on the mechanism of sperm competition and on $r(m)$. If we take as the null expectation that $r(m)$ is dependent only on sperm mass m, the ESS sperm mass (m^*) will not vary with sperm competition risk. This leads to the following obvious (but seldom stated) conclusion: since mass m^* is invariant with risk, but the size-number product v^* increases with risk, the ratio m^*/s^* should decline with risk across populations when resources are equal for those populations. Thus all cases when m^* is decreasing, invariant, or only weakly increasing with q are expected to show declining relationships between m^*/s^* and risk, i.e. there is greater allocation to sperm numbers than to sperm mass as q increases, so that large sperm are most likely to be associated with *low* sperm numbers and *low* sperm competition risk. This is almost always the case in the examples shown in the figures and Tables 1 to 3, where $u = 1$ (the sperm density functions change in direct or inverse proportion to sperm numbers). A declining relation between m^*/s^* and q thus becomes a 'default' expectation. The only case of m^*/s^* increasing with risk at $u = 1$ is that for $f_3 = f_{D2dec}$ in displacement model 2 (Fig. 5i). To generate greater investment in sperm mass than sperm number (m^*/s^* increasing) as risk q increases, we generally need (i) extreme escalation in competitive effects of increased sperm mass as sperm density increases (high u in our models) and (ii) the appropriate relation between $r(m)$ and sperm density, i.e. sperm density must either decrease the slope of $r(m)$ or increase the minimum sperm mass, or both (we were not able to generate m^*/s^* increasing with $f_1 = f_{D2dec}$ in displacement model 2). This can generate an association between large sperm and *high* sperm numbers, and *high* sperm competition risk.

Thus by examining the relation between m^*/s^*, m^*, s^* and q empirically across groups of related species, we can a assemble candidate mechanisms for how sperm density may affect the competitive loading due to sperm mass. Ideally, this may lead to insights about the evolution of sperm size.

9.2. Empirical evidence for size-number trade offs

It has been typically assumed that a decreasing relationship between sperm size and number is evidence of a direct size-number trade off, and conversely that no relation, or a positive relation shows that there is no trade off. Both conclusions can be erroneous if the data are not first corrected for the effects of the extrinsic variables that control ejaculate investment, i.e. risk q, resource level R/D, and displacement capacity ($\alpha/S_{\max}$ or $\alpha/V_{\max}$). To give an illustration of this problem, in Fig. 7 we plot sperm mass against sperm number for given ranges of risk q, holding other parameters (e.g. R/D, $\alpha/S_{\max}$) constant. This is equivalent to obtaining comparative data for a set of species similar in all parameters except sperm competition risk, which is not controlled for, and which varies across the specified range for the species studied. All examples in Fig. 7 are for the case where sperm density changes minimal sperm mass (sperm density function f_3). Figs. 7a and 7b are for the raffle with the same default parameter values as in Fig. 3. If sperm numbers decrease minimum sperm mass ($f_3 = f_{Rinc}$), the relation between mass and number is monotonic decreasing across all q (Fig. 7a shows the range for q = 0.1 to 0.5). This would be interpreted as a typical size-number trade off, yet the result is generated entirely as the effect of the change in ejaculate investment v^* across the difference q values. When sperm numbers increase minimum sperm mass ($f_3 = f_{Rdec}$), the relation between size (mass) and number is reversed, and becomes monotonic increasing across all q (Fig. 7b shows the range for q = 0.1 to 0.5). Across wider ranges of q under certain models, the relation between sperm size (mass) and number can be non-monotonic. For example, Fig. 7c shows results from displacement model 1 with $f_3 = f_{Rinc}$ across the full range for q =0.02 to 0.98. Over the range of q used in Figs. 7a and 7b (shown as unfilled circles), the relation is decreasing, but it is increasing at very low q (< 0.1).

Thus, unless corrected for the effects of extrinsic variables that will affect ejaculate expenditure (notably sperm competition level), evidence for trade offs based on negative relationships between size and number must be regarded with great caution.

9.3. Biological aspects of the models and predictions

Our three sperm competition models represent a continuum in which there is a constraint on space for sperm competing for fertilisations; this continuum exerts strong influences on ejaculate economics (Parker and Pizzari in press). In the raffle (Fig. 1a), there is no space constraint, so that all sperm ejaculated have potentially equal chances to fertilise eggs. However, the potential for competitive interactions between sperm is generally limited. At the other extreme, where there are small sperm-storage organs in the female and males can produce large quantities of sperm cheaply, there is likely to be extensive direct or indirect sperm displacement from the sperm stores (Figs. 1b, 1c), and the displaced sperm will have no chance of fertilisation. In the yellow dung fly, *S. stercoraria*, the dynamics of indirect displacement have been shown to be very similar quantitatively to those of indirect displacement as modelled here (Simmons et al. 1999), so theoretical results may also be analogous over a wide range of conditions. With displacement systems there may be considerable possibility of increasingly severe competitive interactions between sperm with increasing sperm density, leading to the possibility of an increasing ratio of sperm mass/number with increased sperm competition risk.

Direct displacement often generates high P_2 values. For example, direct displacement in the tree cricket, *Truljalia hibinonis*, results in 87.5% of the first males' ejaculate being flushed away by the second males' ejaculate (Ono et al. 1989). In the direct displacement of the rove beetle, *Aleochara curtula,* the spermatophore contains a capsular sperm sac and large amounts of an amorphous secretion. Following insemination, the male's secretions expand hydrostatically, causing the spermatophore to "grow" up the female's spermathecal duct, balloon within the spermatheca, and then burst open, the result of which is to forcibly backflush any resident sperm from previous males from the spermatheca (Gack and Peschke 1994). Indirect sperm displacement in the yellow dung fly, *S. stercoraria*, has been studied in detail. During second matings, while

sperm are ejaculated to the bursa, there is gradual indirect displacement of the ejaculate of previous male(s) from the spermathecae to the bursa, and P_2 matches the proportions of sperm in the spermatheca, typically reaching over 80% by the end of copulation (Simmons et al. 1999).

9.3.1. The raffle model

Biological conditions for the raffle are most likely to be met in external fertilisers such as marine broadcast spawners, externally fertilizing fish and amphibians, where sperm are released into the water, often as the eggs are released. Here, the main advantage of increased sperm mass would probably be in greater speed, or greater longevity. These can generate changes in ESS sperm mass with population sperm competition level since there is a premium in fast fertilisation at high sperm competition, when the proportion of eggs remaining to be fertilised declines quickly (see the intensity models of Ball and Parker 1996, 1997). For example, in externally fertilising cichlids, sperm size determines swimming velocity (Fitzpatrick et al. 2009), which is known to be a major determinant for the outcome of sperm competition in another teleost fish, the Atlantic salmon, *Salmo salar* (Gage et al. 2004). However, unless there are severe competitive effects that change with sperm density, we would not expect the ratio of sperm mass/number (m^*/s^*) to increase in such systems – a decline is much more likely.

In many invertebrate external fertilisers, sperm reach the eggs mainly due to water currents, and the principle selection on sperm mass may be mediated through its relationship with longevity (Levitan 2000). To date, no study has formally tested sperm mass-number relationships across species of external fertilizers. At the intraspecific level, no evidence for a trade-off between size and number was found in *S. salar* (Gage et al. 1998). In externally fertilising myobatrachid frogs, oviposition location has a significant effect on testis size (and hence number of sperm produced), with species ovipositing in foam (i.e. limited fertilization space) having relatively smaller testes (Byrne et al. 2002).

The assumption that the arena for sperm competition is functionally unlimited (Fig. 1a) may also apply to many vertebrates with internal fertilisation, especially large-bodied species, where sperm are minuscule compared to the female reproductive tract. Vertebrate sperm do not differ in absolute size from invertebrate sperm (Hosken 2003); in fact, in many cases they are considerably smaller (Pitnick et al. 2009). This relative size (sperm size/body size) difference may lead to the 'dilution effect', where most sperm become lost inside the female tract, or at least never make it to the site of fertilization, and hence males are selected to produce more sperm (Short 1981, Cummins and Woodall 1985). This resembles the classical argument that increased sperm numbers increase the probability of fertilisation (see Parker 1982). The mechanism in birds has been shown to follow the raffle principle and there is no evidence of displacement (the predominance of paternity of the last male in double matings is a consequence of passive sperm loss; Birkhead 1998). In passerine birds, both sperm number and sperm length increase with sperm competition risk q, and m^*/s^* decreases with q, indicating that the increase in sperm number is relatively greater than that in sperm length, as would be predicted by our models (Immler et al. in prep.).

Interestingly, both sperm number and sperm length have been shown to increase with increasing sperm competition in many different taxa including mammals (Møller 1988; Breed and Taylor 2000; Gomendio and Roldan 1991; Møller 1988a; Møller 1989; but see Gage and Freckleton 2003), birds (Briskie and Montgomerie 1992; Møller 1988b; but see Immler and Birkhead 2007) and reptiles (Tourmente et al. 2009). This positive correlation of both traits with sperm competition level is typically seen as contradicting the existence of a sperm size-number trade off. However, the present analysis (Section 9.2) suggests that to detect trade offs between sperm mass and sperm number, it is crucial to take sperm competition risk into account.

9.3.2. Displacement model 1

The displacement models relate to cases where females store sperm prior to fertilization and the storage space within the female is limited, so that incoming sperm physically displace some

component of the stored sperm, directly or indirectly, removing them from the 'fertilisation set' of sperm within the sperm stores. Such conditions are usually most relevant to internally fertilizing invertebrates, though some vertebrate systems may well approximate to weak displacement. Rather little data is currently available on sperm size-number relationships across species exhibiting sperm displacement.

Displacement model 1 is based on volumetric ejaculate displacement essentially by seminal fluid, and applies to cases of displacement involving a low ratio of sperm mass to seminal fluid volume (Fig. 1b). The volume of the ejaculate (i.e. principally seminal fluid) is the main mechanistic force causing sperm displacement, and sperm mass plays a trivial role. The underlying assumption is that a fixed large volume of uncostly seminal fluid accompanies each sperm, so that small changes in sperm mass (at a constant sperm number) do not significantly alter the degree of displacement, though they attract the cost specified in *Dms*. In contrast, increases in sperm number effect proportionate increases in displacement, because each sperm is accompanied by a fixed amount of seminal fluid.

Cases where males 'flush out' ejaculates of previous competitors by the means of voluminous ejaculates containing large amounts of seminal fluid and hence relatively low densities may be found in both invertebrates and vertebrates, though more commonly in the former. Many cases of volumetric sperm displacement have been documented in insects (see Simmons 2001), though they probably fit better the assumptions displacement model 2.

9.3.3 Displacement model 2

Displacement model 2 was devised to account for cases of volumetric sperm displacement essentially by sperm mass, and (opposite to model 1) applies in its simplest form to cases of displacement involving a low ratio of seminal fluid volume to sperm mass (Fig. 1c). The summed mass of all the sperm is the main mechanistic force causing sperm displacement, so that both changes in sperm mass and in sperm number effect proportionate changes in sperm displacement.

Such conditions are prevalent in insects, where the sperm density is typically very high relative to that of vertebrates, but there is evidence for sperm mass being advantageous in sperm competition in C. elegans (e.g. LaMunyon and Ward 1998, 1999) and bulb mites (Radwan 1996), possibly due to displacement effects.

There is, however, a second interpretation of displacement model 2, which makes it applicable to ejaculates with high volumes of seminal fluid. This is where a fixed volume of seminal fluid accompanies each unit of individual sperm mass, *m*. Thus at a constant sperm number *s*, any increase in sperm mass *m* generates a proportionate increase in ejaculate volume with sperm numbers held constant, giving a proportionate increase in displacement, exactly as would any increase in sperm number with sperm mass held constant. On this interpretation, the effect of costly seminal fluid can be within *Dms* by the constant *D*. Until the mechanisms of sperm and seminal plasma production are better understood, it will not be possible to accurately assess whether model 1 or model 2 is more appropriate, though intuition suggests that model 2 is probably more robust.

Displacement model 2 most closely approximates the selective conditions believed to be occurring in particular in many invertebrate species, most of which have been examined in the insects. It also appears to have relevance to situations in which sperm physically compete for space in the female sperm stores, so that both displacement ability and competitive ability may increase with sperm mass. By way of illustration, we next discuss what is known about the evolution of sperm size, sperm number and their contribution to competitive fertilization success in fruit flies of the genus *Drosophila.* The evolution of sperm length in this lineage has been studied extensively, both comparatively and experimentally, and it has been suggested that in certain species high sperm competition risk has promoted the production and transfer of relatively few, very long sperm.

9.3.4. The Drosophila system

There is remarkable variation in sperm length (about 180 fold) across *Drosophila* species; at one extreme, *D. bifurca* have evolved giant sperm that are 58.3 mm long, or 20 times the total body

length of males whilst *D. melanogaster* sperm are only 1.90 mm long (Pitnick et al. 1995). Production of relatively long sperm is energetically costly (Pitnick et al. 1995; Pitnick 1996). Sperm length has been demonstrated to trade off with sperm number: specifically, after statistically controlling for the total investment in spermatogenesis, there is a highly significant negative relationship across species between sperm length and the number of sperm produced and transferred to females (Pitnick 1996; Bjork and Pitnick 2006). Assuming that total investment in spermatogenesis is positively correlated with sperm competition risk, this finding fits well with our present predictions, since the product $m^* s^*$ is constant at a given q. Females of most species are promiscuous, with some of the highest female remating rates (i.e. up to several times per day) observed in those species where males produce the longest sperm (Pitnick and Markow 1994a, 1994b; Bjork and Pitnick 2006). This suggests that higher sperm competition risk is selecting for longer sperm. While our models can readily giant sperm at very low sperm competition, this is characterised by both m^* and m^*/s^* decreasing with q (see Figs. 3 to 5); in *Drosophila*, both m^* and m^*/s^* are increasing with q, consistent with increasing sperm competition risk (and sperm density) favouring longer sperm (Immler et al. manuscript).

Of critical consideration for our displacement model 2, (i) female *Drosophila* have limited sperm-storage capacity (about 500 in *D. melanogaster* (Manier et al., manuscript) and 40 in *D. bifurca* (Luck et al. 2007)), (ii) males typically transfer more sperm than females are capable of storing (about 1500 in *D. melanogaster* (Miller and Pitnick 2002) and 140 in *D. bifurca* (Luck et al. 2007)) and (iii) there is a strong pattern of correlated evolution between the length of sperm and length of the female's primary sperm-storage organ, the seminal receptacle, observed across both geographic populations (Pitnick et al. 2003) and species (Pitnick et al. 1999). Experimental evolution studies with *D. melanogaster* suggests that these interacting, sex-specific traits coevolve, that second male sperm precedence is due in part to displacement of resident sperm by second male sperm, that longer sperm are better at displacing and resisting being displaced by shorter sperm, and that the fitness advantage of having relatively long sperm critically depends upon interaction with

the length of the female's seminal receptacle (Miller and Pitnick 2002; Pattarini et al. 2006). Moreover, an experiment with *D. melanogaster* in which sperm length and the number of sperm inseminated were varied in a fully factorial design revealed that both sperm length and number independently explain a significant amount of the variation in P_2. It is particularly noteworthy, however, that sperm length appeared to be the more important explanatory variable, and that there was a significant interaction between sperm length and number, indicating that the sperm length becomes increasingly important when sperm numbers are reduced. Given that directional evolution for increasing sperm length entails an increase in total investment in testes and thus enhanced direct trade off with sperm number (Pitnick 1996; Immler et al. manuscript), a consequence of the length-number interaction on P_2 is that selection on sperm size in lineages will have a positive, self-reinforcing momentum.

P_2 tends to be high (e.g., 0.80-0.90 in *D. melanogaster* (e.g., Brown et al. 2004) and 0.95-0.98 in *D. bifurca* (Luck et al. 2007)), and this is attributable to greater proportional representation of second male sperm in the female's sperm-storage organs, as in our model. The preponderance of second male sperm results from the combination of (i) females only having the capacity to store a fraction of the sperm inseminated, (ii) many of the first male sperm having been used for egg fertilization during the remating interval, and (iii) indirect displacement of resident sperm from the storage organs, triggered by second male seminal fluids and resulting from mass displacement by second male sperm, followed by (iv) female ejection of all "excess" first and second male sperm from her reproductive tract (Snook and Hosken 2004; Manier et al., manuscript). Importantly, our models explore evolution of sperm traits relative to varying sperm competition risk, rather than intensity. Even though females of many *Drosophila* species appear to remate frequently (e.g., *D. melanogaster* females collected in the wild are estimated to have had 1.82 – 2.44 sexual partners; Harshman and Clark 1998; Jones and Clark 2003), there is negligible persistence of a given male's sperm beyond two additional matings by his mate (Morrow et al. 2005; Bjork et al. 2007); hence it is essentially only two males' sperm that are ever competing at a given time.

Although both experimental and comparative evidence strongly support the contention that very long sperm in *Drosophila* is an adaptation to acute postcopulatory sexual selection (Miller and Pitnick 2002; Bjork and Pitnick 2006; Luck et al. 2007), because longer sperm are more effective at displacing rival sperm (Miller and Pitnick 2002; Pattarini et al. 2006), the actual number of competitor sperm competing for egg fertilizations declines as sperm length increases, since P_2 increases. Moreover, because length of the female SR appears to bias sperm use (imposes selection on sperm length) in the manner of a "psychophysical" (Hall et al. 2000) or open-ended female preference (in the manner of discriminating *against* shorter sperm, with the threshold of discrimination increasing with seminal receptacle length), we suggest that the y-intercept of sperm length may increase with increasing risk of sperm competition (q) as assumed in our model when $m_{\min}$ increases with increasing sperm density (Fig. 2c). This assumption, coupled with that of displacement by sperm mass (displacement model 2), generates much the most likely conditions favouring the evolution of very long sperm under high sperm competition risk, q. While the present models can predict the observed increase in both sperm mass (m^*) and size/number ratio (m^*/s^*) with q, they fail to predict an observed decline in sperm numbers (s^*) over the higher part of the range of q (Immler et al., in prep.). This decline in sperm numbers may require an alternative explanation.

9.4. The evolution of P2

Whether a female remates on encounter with a male can result in sexual conflict in which it pays the male to mate but not the female: resolution of this conflict depends on the sexual asymmetry in the relative value of winning and the relative power exerted, and can range between 'male wins' and 'female wins' outcomes (Parker 2006). We do not consider female control of mating or female influence on P_2 in the present paper. However, if the female controls mating, and

remates because she prefers the current male, she benefits most if P_2 is high, which leads to a female-control explanation of observed P_2 values.

The present analysis leads to an explanation of observed P_2 values when there is male control of mating. In our displacement models, ESS displacement always results in $P_2 > 0.5$, and P_2 always increases with q (See Section 8). Including an extrinsic loading related to mating order may allow $P_2 < 0.5$ (the effect of extrinsic loadings is complex, see Ball and Parker 2000); this has not been investigated in the present analysis since our aim was to examine sperm size (mass) and number in a fair raffle. However, it is interesting to note that in Simmons' (2001) monograph on insect sperm competition, the distribution of mean P_2 values for 133 insect species show the vast majority with $P_2 > 0.5$ (see also Parker 1970). The present analysis must be regarded as one male-control explanation for the observed predominance of $P_2 > 0.5$ values. A second explanation could be that first ejaculates may have sustained passive sperm loss due either to random sperm mortality or loss from the sperm stores before a second mating occurs; this can not, however, explain $P_2 > 0.5$ in experiments where the second mating follows immediately after the first.

Our displacement models also predict increasing P_2 with increasing risk of sperm competition (q). Whereas in vertebrates, sperm precedence often appears to follow the raffle principle or various modifications of it, such as passive sperm loss (e.g. birds, Birkhead et al. 1995; Colegrave et al. 1995, Birkhead 1998) or sperm store filling then random sperm use (in the rough-skinned newt, *Taricha granulosa* (Jones et al. 2002), displacement mechanisms are common in invertebrate taxa (Simmons 2001). In insects, second males to mate may displace sperm of previous males by various means such as 'sperm flushing' (see Simmons 2001 for review). The displacement of one ejaculate by another may have two mechanistic bases: either the ejaculate as a whole 'flushes' out the previous ejaculate (displacement model 1; e.g. Gack and Peschke 1994; Simmons et al. 1999), or sperm of different males compete directly for space in the sperm stores, since sperm size is a major determinant of sperm displacement outcome as well as fertilization outcome (displacement

model 2; e.g. Radwan 1996; La Munyon and Ward 1999; Miller and Pitnick 2002; Pattarini et al. 2006). The two displacement models address the former two scenarios.

Our displacement models assume that there is no extrinsic competitive loading, i.e. no mating order effect increasing or diminishing the chances of fertilisation success of the second male compared to the first male. This assumption should not, *a priori*, affect the prediction of a positive association between P_2 and q. Empirical for this positive association between P_2 and q has not yet been provided. Variation of P_2 within species is high (Simmons 2001), and numerous studies in different taxa have investigated P_2 in relation to varying (often) interacting factors including time interval between first and second mating (Drnevich et al. 2000; Blyth and Gilburn 2005; Fricke et al. 2008), male and/or female condition and age (e.g. LaMunyon 2001; Fedina and Lewis 2004) and male and female genotypes (e.g. Civetti and Clark 2000; Bretman et al. 2004; Blyth and Gilburn 2005). To demonstrate the predicted relationship between P_2 and q it will be important to perform experiments under controlled, standardised conditions in various species, such as *Drosophila*.

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Legends to the Figures

Fig. 1. The three mechanisms of sperm competition investigated. (a) Raffle. Males ejaculate into an unconstrained space from which sperm are drawn for fertilization; there is no displacement of previous sperm during ejaculation. The ESS sperm mass is m^* and sperm number is s^*. Mutations affect either sperm mass or sperm numbers, but not both simultaneously. In the example shown, the mutant male 2 has larger sperm ($m > m^*$). Fertilisations are drawn from the sperm available after both males have ejaculated, after the loaded raffle principle in which the raffle is loaded by sperm mass (see text). (b) Displacement mainly by seminal fluid. Males ejaculate sequentially, and during ejaculation of the second male there is continuous displacement of previously-stored sperm from the constrained storage space in the female tract following the model of direct displacement with instant mixing (Parker & Simmons 1991). Each sperm is transferred in a fixed volume of seminal fluid that is much larger than the sperm mass, so that deviations in sperm mass have a negligible effect on displacement. (c) Displacement mainly by sperm mass. Displacement is as in (b), except that the seminal fluid volume per sperm is negligible (or alternatively, seminal fluid increases in proportion to sperm mass), so that for a fixed number of sperm, displacement increases with sperm mass. In (b) and (c), once ejaculation of the second (last) male is complete, the fertilisation follows a raffle loaded by sperm mass as in (a).

Fig. 2. Changes in ESS sperm mass when sperm numbers change the form of $r(m,\mathrm{I})$ in the raffle model, predicted by the marginal value theorem tangent method from equation (13). The solid curve is $r(m,\mathrm{I})$, the competitive weight of a sperm in relation to its mass m, at a given ESS sperm number s^*, with the exponential form shown in equation (30). The ESS sperm mass, m^*, is the value of m beneath each tangent to the curve (shown by the open or filled circles). In each figure, the heavy continuous curve uses a set of default values for the three functions of s^*, f_1, f_2, f_3, in (30) which define the ESS sperm mass (m value beneath the filled circle on the continuous curve).

The two thinner curves show the effect of unilaterally increasing (broken curve) or decreasing (broken-dotted curve) the value of one of the functions f_1, f_2, f_3 to show how this alters the ESS sperm mass (m value beneath the open circle on the broken or broken-dotted curve). (a) Effect of varying f_1; i.e. sperm numbers change the asymptote of $r(m,\mathrm{I})$. Whether the asymptote increases or decreases with increased sperm numbers, this does not affect the ESS sperm mass, m^*. (b) Effect of varying f_2; i.e. sperm numbers change the rate at which $r(m,\mathrm{I})$ approaches its asymptote. If increasing sperm numbers increase the rate of approach (broken curve), this decreases ESS sperm mass, m^*. If increasing sperm numbers decrease the rate of approach (broken-dotted curve), this increases ESS sperm mass, m^*. Modified from Pizzari & Parker (2009). (c) Effect of varying f_3; i.e. sperm numbers change the mimimum sperm mass for fertilisation (the intercept of $r(m,\mathrm{I})$ on the m axis. If increasing sperm numbers increase minimum sperm mass (broken curve), this increases ESS sperm mass, m^*. If increasing sperm numbers decrease the minimum sperm mass (broken-dotted curve), this decreases ESS sperm mass, m^*.

Fig. 3. Relation between ESS sperm mass (continuous curve) or number (broken curve) and sperm competition risk in the raffle model. (a) Case where sperm numbers *increase* the rate at which $r(m,\mathrm{I})$ rises to its asymptote, i.e. (30b) with $f_2 = f_{Rinc}$ as in (31a). (b) Case where sperm numbers *decrease* the rate at which $r(m,s^*)$ rises to its asymptote, i.e. (30b) with $f_2 = f_{Rdec}$ as in (31b). (c) Relation between ESS sperm mass/number and sperm competition risk for the examples in (a) where the sperm density function is $f_2 = f_{Rinc}$, and (b) where $f_2 = f_{Rdec}$. (d) Case where sperm numbers *increase* the minimum sperm mass ($m_0 = f_3 m_{\min}$), i.e. (30c) with $f_3 = f_{Rinc}$ as in (31a). Curves are for $u = 1$ and $u = 10$. (e) Case where sperm numbers *decrease* the minimum sperm mass ($m_0 = f_3 m_{\min}$), i.e. (30c) with $f_3 = f_{Rdec}$ as in (31b). (f) Relation between ESS sperm mass/number or sperm competition risk for the examples in (d) where the sperm density function is $f_3 = f_{Rinc}$, and (e) where $f_3 = f_{Rdec}$. In (a), (b), (d) and (e) the dotted curve is the product, $v^* = m^* s^*$, which is equal

for all cases, following equation (12). Parameters (unless otherwise stated) are $R = 10$, $D = 1$, $b = 1$, $m_{\min} = 0.1$, $u = 1$.

Fig. 4. Relation between ESS sperm mass (continuous curve) or number (broken curve) and sperm competition risk in displacement model 1. (a) Case where sperm numbers *increase* the rate at which $r(m,\mathrm{I})$ rises to its asymptote, i.e. (30b) with $f_2 = f_{D1inc}$ as in (32a). (b) Case where sperm numbers *decrease* the rate at which $r(m,s^*)$ rises to its asymptote, i.e. (30b) with $f_2 = f_{D1dec}$ as in (32b). (c) Relation between ESS sperm mass/number and sperm competition risk for the examples in (a) where the sperm density function is $f_2 = f_{D1inc}$, and (b) where $f_2 = f_{D1dec}$. (d) Case where sperm numbers *increase* the minimum sperm mass ($m_0 = f_3 m_{\min}$), i.e. (30c) with $f_3 = f_{D1inc}$ as in (32a). (e) Case where sperm numbers *decrease* the minimum sperm mass ($m_0 = f_3 m_{\min}$), i.e. (30c) with $f_3 = f_{D1dec}$ as in (32b). In the grey shaded area the ESS appears to shift discontinuously to lower mass and higher number (see text). (f) Relation between ESS sperm mass/number or sperm competition risk for the examples in (d) where the sperm density function is $f_3 = f_{D1inc}$, and (e) where $f_3 = f_{D1dec}$. The curve for $u = 10$ with $f_3 = f_{D1inc}$ is also included. In (a), (b), (d) and (e) the dotted curve is the product, $v^* = m^* s^*$. In (a), (b), (d) and (e) the thin dotted v^* curves are for $\alpha / S_{\max} = 1$ and 1/10 as indicated. Parameters (unless otherwise stated) are $R = 10$, $D = 1$, $b = 1$, $m_{\min} = 0.1$, $u = 1$, $\alpha = 1$, $S_{\max} = 100$.

Fig. 5. Relation between ESS sperm mass (continuous curve) or number (broken curve) and sperm competition risk in displacement model 2. (a) Case where sperm numbers *increase* the asymptote of $r(m,\mathrm{I})$, i.e. (30a) with $f_1 = f_{D2inc}$ as in (33a). (b) Case where sperm numbers *decrease* the asymptote of $r(m,\mathrm{I})$, i.e. (30a) with $f_1 = f_{D2dec}$ as in (33b). We were unable to iterate solutions for m^*, s^* in the grey shaded area at low q (see text). (c) Relation between ESS sperm mass/number

and sperm competition risk for the examples in (a) where the sperm density function is $f_1 = f_{D2inc}$, and (b) where $f_1 = f_{D2dec}$. (d) Case where sperm numbers *increase* the rate at which $r(m,\mathrm{I})$ rises to its asymptote, i.e. (30b) with $f_2 = f_{D2inc}$ as in (33a). (e) Case where sperm numbers *decrease* the rate at which $r(m,s^*)$ rises to its asymptote, i.e. (30b) with $f_2 = f_{D2dec}$ as in (33b). (f) Relation between ESS sperm mass/number and sperm competition risk for the examples in (d) where the sperm density function is $f_2 = f_{D2inc}$, and (e) where $f_2 = f_{D2dec}$. (g) Case where sperm numbers *increase* the minimum sperm mass ($m_0 = f_3 m_{\min}$), i.e. (30c) with $f_3 = f_{D2inc}$ as in (33a). (h) Case where sperm numbers *decrease* the minimum sperm mass ($m_0 = f_3 m_{\min}$), i.e. (30c) with $f_3 = f_{D2dec}$ as in (33b). (i) Relation between ESS sperm mass/number or sperm competition risk for the examples in (g) where the sperm density function is $f_3 = f_{D2inc}$, and (h) where $f_3 = f_{D2dec}$. In (a), (b), (d), (e), (g) and (h), the dotted curves are the product, $v^* = m^* s^*$; the thicker v^* curve is for $\alpha/V_{\max}$ = 1/100 and the thinner curve is for $\alpha/V_{\max}$ = 1/1 as indicated. Parameters (unless otherwise stated) are R = 10, D = 1, b = 1, $m_{\min}$ = 0.1, u = 1, α = 1, $V_{\max}$ = 100.

Fig. 6. Relation between ESS P_2 value and sperm competition risk in the three models. (a) Displacement model 1 with sperm density function f_2, and (b) displacement model 1 with sperm density function f_3. The continuous curves are for the increasing sperm density functions f_{D1inc}, f_{D2inc}, and the broken curves are for decreasing sperm density functions f_{D1dec}, f_{D2dec}. (c) Displacement model 2. All models have the same relation between P_2 value and sperm competition risk at a given displacement capacity ($\alpha/V_{\max}$) or resource level (R/D).Parameters are R = 10, D = 1, b = 1, $m_{\min}$ = 0.1, u = 1. Two displacement capacities are shown ($\alpha/V_{\max}$ = 1/100 and 1).

Fig. 7. Relation between sperm mass and sperm number using sperm density function f_3 across a range of sperm competition risk. (a) Raffle when sperm numbers decrease minimum sperm mass

($f_3 = f_{Rdec}$), across the range for q = 0.1 to 0.5). (b) Raffle when sperm numbers increase minimum sperm mass ($f_3 = f_{Rinc}$), across the same range for q). (c) Displacement model 1 when sperm numbers increase minimum sperm mass ($f_3 = f_{D1inc}$), across the full range for q. The open circles are for values within the range q = 0.1 to 0.5. Parameter values as in Fig. 3 (raffle) and Fig. 4 (displacement model 1).

Table 1. Raffle model. Differences in trait response to f_{Rinc}, f_{Rdec} are highlighted in grey. Convention: v = effect varies with q; change in trait with unilateral increase in parameter from the default values given in Fig. 3 = + (increase), - (decrease).

Model	Ejaculate trait	Relation with parameter: q	u	b	m_{min}	R/D	Comments
(a) sperm density function f_2							
f_{Rinc} - s increases rate of rise to asymptotic r	m^*	-	v	-	+	-	Directly proportional to m_{min}
	s^*	+	v	+	-	+	Inversely proportional to m_{min}
	m^*s^*	+	constant	constant	constant	+	Independent of r parameters; directly proportional to R/D
	m^*/s^*	-	-	-	+	-	
f_{Rdec} - s decreases rate of rise to asymptotic r	m^*	+	v	+	+	+	
	s^*	+	v	-	-	+	
	m^*s^*	+	constant	constant	constant	+	Independent of r parameters; directly proportional to R/D
	m^*/s^*	-	-	-	+	-	
(b) sperm density function f_3							
f_{Rinc} - s increases minimum sperm size	m^*	+	v	+	+	+	
	s^*	+	v	-	-	+	
	m^*s^*	+	constant	constant	constant	+	Independent of r parameters; directly proportional to R/D
	m^*/s^*	-	v	+	+	-	
f_{Rdec} - s decreases minimum sperm size	m^*	-	-	-	+	-	
	s^*	+	+	+	-	+	
	m^*s^*	+	constant	constant	constant	+	Independent of r parameters; directly proportional to R/D
	m^*/s^*	-	-	-	+	-	

Table 2. Displacement model 1. Differences in trait response to f_{Rinc}, f_{Rdec} are highlighted in grey. Convention: v = effect varies with q; change in trait with increase in parameter = + (increase), - (decrease).

Model	Ejaculate trait	Relation with parameter: q	u	α/S_{max}	b	m_{min}	R/D	Comments
(a) sperm density function f_2								
f_{D1inc} - s increases rate of rise to asymptotic r	m^*	-	v	+	-	+	-	
	s^*	+	v	-	+	-	+	
	m^*s^*	+	almost constant	-	almost constant	almost constant	+	almost invariant with u, b, and m_{min}
	m^*/s^*	-	v	+	-	+	-	
	P_2	+	v	+	+	-	+	
f_{D1dec} - s decreases rate of rise to asymptotic r	m^*	+	v	-	+	+	+	
	s^*	+	v	+	-	-	+	
	m^*s^*	+	almost constant	-	almost constant	almost constant	+	almost invariant with u, b, and m_{min}
	m^*/s^*	-	v	-	+	+	-	
	P_2	+	v	+	-	-	+	
(b) sperm density function f_3								
f_{D1inc} - s increases minimum sperm size	m^*	+	v	-	+	+	+	
	s^*	+	v	+	-	-	+	
	m^*s^*	+	almost constant	-	almost constant	almost constant	+	almost invariant with u, b, and m_{min}
	m^*/s^*	-	v	-	+	+	-	
	P_2	+	v	+	-	-	+	
f_{D1dec} - - s decreases minimum sperm size	m^*	-	v	+	-	+	-	
	s^*	+	v	-	+	-	+	
	m^*s^*	+	almost constant	-	almost constant	almost constant	+	almost invariant with u, b, and m_{min}
	m^*/s^*	-	v	+	-	+	-	
	P_2	+	v	+	+	-	+	

Table 3. Displacement model 2. Differences in trait response to f_{Rinc}, f_{Rdec} are highlighted in grey. Convention: v = effect varies with q; change in trait with increase in parameter = + (increase), - (decrease); i = response is independent of the parameter; +?, -? = responses obtainable only over a small range of the parameter.

Model	Ejaculate trait	Relation with parameter: q	u	α/V_{max}	b	m_{min}	R/D	Comments
(a) sperm density function f_1								
	m^*	+	-	v	i	+	+	
	s^*	+	+	-	i	-	+	Almost invariant with α/V_{max}
f_{D2inc} - v increases asymptotic r	m^*s^*	+	constant	-	i	constant	+	Proportional to R/D
	m^*/s^*	-	-	v	i	+	-	
	P_2	+	constant	+	i	constant	+	
	m^*	-	+	-	i	+	-	
	s^*	+	-	+	i	-	+	
f_{D2dec} - v decreases asymptotic r	m^*s^*	+	constant	-	i	constant	+	Proportional to R/D
	m^*/s^*	-	+	-	i	+	-	
	P_2	+	constant	+	i	constant	+	
(b) sperm density function f_2								
	m^*	-	v	v	-	+	-	Almost invariant with α/V_{max}
f_{D2inc} - s increases rate of rise to asymptotic r	s^*	+	v	v	+	-	+	Almost invariant with α/V_{max}
	m^*s^*	+	constant	-	constant	constant	+	Proportional to R/D
	m^*/s^*	-	v	v	-	+	-	Almost invariant with α/V_{max}
	P_2	+	constant	+	constant	constant	+	
	m^*	+	-	v	+	+	+	Almost invariant with α/V_{max}, q, R/D
f_{D2dec} - s decreases rate of rise to asymptotic r	s^*	+	+	-	-	-	+	Almost invariant with α/V_{max}; almost proportional to R/D
	m^*s^*	+	constant	-	constant	constant	+	Proportional to R/D
	m^*/s^*	-	-	+	+	+	-	Almost invariant with α/V_{max}
	P_2	+	constant	+	constant	constant	+	
(c) sperm density function f_3								
	m^*	+	- ?	v	+	+	+	Almost invariant with q
f_{D2inc} - s increases minimum sperm size	s^*	+	+ ?	v	-	-	+	
	m^*s^*	+	constant	-	constant	constant	+	Proportional to R/D
	m^*/s^*	-	+ ?	v	+	+	+	
	P_2	+	constant	+	constant	constant	+	
	m^*	-	+ ?	+	-	+	-	
f_{D2dec} - - s decreases minimum sperm size	s^*	+	- ?	-	+	-	+	
	m^*s^*	+	constant	-	constant	constant	+	Proportional to R/D
	m^*/s^*	+	-?	+	-	+	-	
	P_2	+	constant	+	constant	constant	+	

RAFFLE
loaded by sperm size