



Sperm competition games: sperm selection by females

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Abstract

We analyse a co-evolutionary sexual conflict game, in which males compete for fertilizations (sperm competition) and females operate sperm selection against unfavourable ejaculates (cryptic female choice). For simplicity, each female mates with two males per reproductive event, and the competing ejaculates are of two types, favourable (having high viability or success) or unfavourable (where progeny are less successful). Over evolutionary time, females can increase their level of sperm selection (measured as the proportion of unfavourable sperm eliminated) by paying a fecundity cost. Males can regulate sperm allocations depending on whether they will be favoured or disfavoured, but increasing sperm allocation reduces their mating rate.

The resolution of this game depends on whether males are equal, or unequal. Males could be equal: each is favoured with probability, p , reflecting the proportion of females in the population that favour his ejaculate (the ‘random-roles’ model); different males are favoured by different sets of females. Alternatively, males could be unequal: given males are perceived consistently by all females as two distinct types, favoured and disfavoured, where p is now the frequency of the favoured male type in the population (the ‘constant-types’ model). In both cases, the evolutionarily stable strategy (ESS) is for females initially to increase sperm selection from zero as the viability of offspring from unfavourable ejaculates falls below that of favourable ejaculates. But in the random-roles model, sperm selection decreases again towards zero as the unfavourable ejaculates become disastrous (i.e. as their progeny viability decreases towards zero). This occurs because males avoid expenditure in unfavourable matings, to conserve sperm for matings in the favoured role where their offspring have high viability, thus allowing females to relax sperm selection. If sperm selection is costly to females, ESS sperm selection is high across a region of intermediate viabilities. If it is uncostly, there is no ESS in this region unless sperm limitation (i.e. some eggs fail to be fertilized because sperm numbers are too low) is included into the model. In the constant-types model, no relaxation of sperm selection occurs at very low viabilities of disfavoured male progeny. If sperm selection is sufficiently costly, ESS sperm selection increases as progeny viability decreases down towards zero; but if it is uncostly, there is no ESS at the lowest viabilities, and unlike the random-roles model, this cannot be stabilized by including sperm limitation.

Sperm allocations in the ESS regions differ between the two models. With random roles, males always allocate more sperm in the favoured role. With constant types, the male type that is favoured allocates less sperm than the disfavoured type. These results suggests that empiricists studying cryptic female choice and sperm allocation patterns need to determine whether sperm selection is applied differently, or consistently, on given males by different females in the same population.

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1. Introduction

Sperm competition (competition between the ejaculates of two or more males for the fertilization of a given set of ova; [Parker, 1970](#)) is a pervasive phenomenon in biology and is the subject of several books or reviews ([Smith, 1984](#); [Baker and Bellis, 1995](#); [Birkhead and](#)

[Møller, 1992, 1998](#); [Simmons, 2001](#)). A theoretical basis for understanding the evolution of ejaculate characteristics under sperm competition has been developed over the past decade or so (reviewed by [Parker, 1998](#)). Much of it concerns male adaptations and the evolution of sperm allocation (the expenditure on a given ejaculate) under varying conditions experienced by competing males. Where female influences on male sperm allocation have been studied, these have been assumed to be non-strategic and uniform with respect to the competing males ([Greef and Parker, 2000](#)). Empirical interests have shifted recently towards female influences, and in

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particular to ways in which females may exert control over paternity against male interests (Eberhard, 1996, Birkhead, 1998).

The present paper examines two evolutionary games in which females exert a preference for certain males' sperm by destroying (or otherwise disadvantaging) the sperm of their competitors. We assume that this mechanism (destruction of unfavourable sperm) has some costs to the female, but also confers benefits since the offspring of favoured males have higher viability (or other fitness-related characteristics) than the disfavoured males. Though our focus here is on costly physiological mechanisms of sperm selection, biased paternity can also be caused by behavioural mechanisms of ejaculate ejection (Eberhard, 1996), which may be less costly to the female.

We seek evolutionarily stable strategy (ESS; Maynard Smith, 1982) solutions for sperm competition games involving two strategic components that are adjusted over evolutionary time. Females can increase their 'sperm selectivity', i.e. the loading against disfavoured males, by increasing the probability that given disfavoured sperm are eliminated. This increases female costs, but biases paternity towards the favoured male. Males can increase the number of sperm ejaculated, which increases the probability that their sperm will be used at fertilization. We assume that fertilization success is determined by a lottery between the sperm available (the 'raffle principle'; Parker, 1982) so that if male i ejaculates s_i sperm in competition with \hat{s} from other males, he gains $s_i/(s_i + \hat{s})$ of the eggs, if the lottery is fair. Thus our games involve sperm competition (males compete by numerical sperm predominance) and also sexual conflict and sexual arms races (females can escalate their sperm selectivity, and males can retaliate by increasing their sperm allocation).

We examine two cases. In the first, the "random-roles" model, each male may have sperm that are favoured by some females and disfavoured by other females. Though the sets of females that favour given males may differ, the prospects of all males are assumed to be equal. In the second model, the "constant-types" model, there are two distinct types of male in the population, and all females favour the sperm of one male type and disfavour the other type. Thus the prospects of the two male types therefore differ. These cases correspond to the random roles and constant roles models of Parker (1990) for sperm competition games without the element of sperm selection. We use "constant types" rather than "constant roles" to stress that given males always experience a given condition (Mesterton-Gibbons 1999a; Ball and Parker 2000).

The results here are compared with previous models that have no component of sperm selection. In the present paper we do not examine cases where males can be related to the females they mate with. This is likely to

be an important component of sperm selection by females (e.g. see Simmons, 2001), and will be dealt with elsewhere.

The next Sections 2–5 outline our modelling analyses. Section 2 specifies assumptions: in summary, females can detect sperm that if used for fertilization reduces offspring viability. By selective elimination, they allow only fraction r of unfavourable sperm to compete for fertilization. There is a cost, c , to the female for the biological mechanism of increasing r . Males compete against each other, and against the female's sperm selection, by increasing their sperm allocation, which has a cost in terms of the number of matings achieved. Section 3 derives the ESS sperm allocations for the random-roles model, i.e. sperm numbers ejaculated by a given male in each of its two roles (favoured or disfavoured). Section 4 derives the ESS sperm allocations for the constant-types model, i.e. sperm numbers ejaculated by a male of the favoured type, and by a male of the disfavoured type. Section 5 outlines the computational procedure, and Section 6 presents some numerical results.

2. Assumptions of the models

In both models, each female copulates with exactly two males before her eggs are fertilized.

2.1. The random-roles model

In the random-roles model (Fig. 1a), each male meets a proportion p of females that treat him as a favoured male, and a proportion $(1 - p)$ that treat him as a disfavoured male. Thus although males may differ in the sense that a different set of females treat given males as favoured, at the ESS all males have equal fitness. Each male can respond to cues which give him perfect information about his role, he can therefore ejaculate strategically as a favoured male with probability p , or a disfavoured male with probability $(1 - p)$. But we assume that he has no knowledge of the role of his competitor. Let role 1 be the favoured role, and role 2 the disfavoured role. Because roles 1 and 2 represent a given female's perspective of the males which mate with her, she may treat both males as being disfavoured, so a male ejaculating in role 2 can either compete against another disfavoured male in role 2, or against a favoured male in role 1; similarly, a male in role 1 may compete with another male in role 1 or with a male in role 2 (Fig. 1a).

2.2. The constant-types model

In the constant-types model (formerly called the constant-roles model; (Parker 1990), males are of two

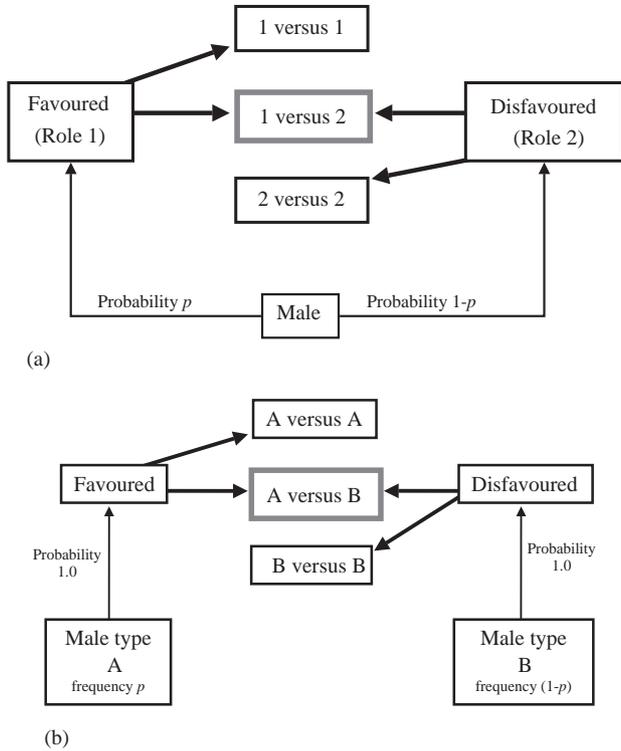


Fig. 1. Comparison of the structure of the two models. (a) Random-roles model. Each male has the probability p of being favoured by a given female (role 1), and probability $(1-p)$ of being disfavoured by a given female (role 2). A male may compete against another male in the same role, or against a male in the other role. (b) Constant-types model. Males are of two phenotypes, A (favoured) and B (disfavoured), and the frequency of A males in the population is p . A given male may compete against another male of the same type, or against a male of the other type.

distinct phenotypes: A (favoured males) and B (disfavoured males). A occurs with frequency p and B with frequency $(1-p)$. All males do not now have equal prospects; A males have better prospects than B males because all females have a similar sperm selectivity pattern for A and B . The game structure is therefore slightly different (Fig. 1b) because a given male only has one ejaculation strategy, not two as in the random-roles model. This strategy is shaped by competition from similar and dissimilar males (A competes against A or B , and B against B or A).

2.3. Progeny costs due to disfavoured males

In both models, each female copulates with two males, and the sperm from each male vies for reproductive success via the raffle process (Parker, 1982). We assume that there is an evolutionary reason for males to be considered disfavoured. This relates to a cost in terms of the progeny they produce with the female they mate with. The number of offspring arising from each disfavoured male is reduced by a factor Δ to

account for their lower viability and/or reproductive success.

2.4. Sperm selection

Sperm selectivity is incorporated by a loading factor r , controlled by the females, which acts against the sperm of disfavoured males so that when such males deliver s sperm, these act in the fertilization raffle effectively as rs sperm where $0 \leq r \leq 1$. To effect this loading, a female has to use up some resources (e.g. for mammals these may be seen as resources expended on immunologically active cells that consume sperm within the female tract; Birkhead et al., 1993). Sperm selectivity costs are accounted for by the female having the number of eggs she produces reduced by a factor (E'/E) where E is the number of eggs produced when there is no reduction and E' when there is a reduction. There could be many forms taken for this factor, but we expect that progeny losses would escalate as the sperm selectivity, r , increases. We use the explicit form

$$E'/E = [1 - c(1 - r)^2], \tag{1}$$

where c is a positive constant. An increase in c has the effect of increasing the costs of a given amount of selectivity r (Fig. 2). This form has a continuous first derivative at $r = 1$, i.e. when there is no sperm reduction, which is a necessary condition on E'/E . We seek an ESS level of selectivity, r^* .

No conscious actions are implied by the female's control of sperm selectivity; the preference for sperm is likely to be the product of evolution of sperm recognition systems at the molecular level. The costs of sperm selectivity are therefore felt throughout by

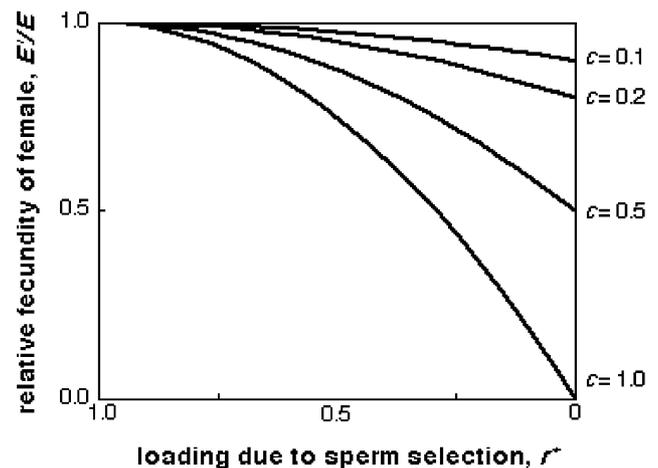


Fig. 2. Costs of sperm selection. To increase sperm selection against disfavoured males, the female reduces r , which increases the loading against disfavoured sperm. The more she reduces r , the greater the reduction in her relative fecundity, E'/E , as defined by Eq. (1). The fecundity cost of r is increased by increasing parameter c .

females, not simply when disfavoured males are encountered.

2.5. Sexual conflict

Thus our models allow males, over evolutionary time, to vary their sperm allocation in response to the female strategies for sperm selectivity and to the sperm allocation strategies of competing males, and females to vary their selectivity in response to the sperm allocation patterns of males. They therefore simulate the outcome of sexual conflict and a sexual arms race (Parker, 1979).

2.6. Sperm limitation

Significant sperm limitation occurs commonly in a few groups where sperm numbers around the egg can typically be too small to give high fertilization success (e.g. see Levitan, 1998), and instances of some reduction in fertility through sperm limitation are probably widespread (e.g. see Wedell et al., 2002). Such effects have an interesting effect on the calculations, which we shall see later. Although sperm limitation, when significant, will affect ESS solutions (Mesterton-Gibbons, 1999a; Ball and Parker, 2000), in the majority of biological situations they are weak or insignificant, and can be ignored. This is what we do at first; however, they may be required to make our mathematical models behave smoothly, and this turns out to be the case.

We first describe the models without sperm limitation and then later describe how these were modified to take sperm limitation into account. Non-mathematical readers may prefer at this point to move directly to the biological discussion (Section 7).

3. Analysis of the random-roles model

Each male has two roles, 1 and 2, which he occupies randomly, role 1 being occupied with a probability p . A male has a choice of how many sperm he ejaculates in each role: we write this as a strategy (s_1, s_2) . An ESS male's strategy is written (s_1^*, s_2^*) . The difference between the roles is that in role 2, the male is disfavoured by having his sperm reduced by a factor r due to the female's sperm selection. Thus if one male occupies role 1 and the other male role 2 and they both play the same strategy, the female loads the fertilization raffle in favour of the male in role 1, so that the two males gain fertilizations with probabilities $s_1/(s_1 + rs_2)$ and $rs_2/(s_1 + rs_2)$, respectively. If both males occupy the same role, they gain 0.5 fertilizations each.

Consider a male who plays (s_1, s_2) when all other males are ESS. We suppose that all females can produce the same number of eggs, i.e. E is a constant, (see Eq. (1)

for E'/E). We define the expression A as

$$A(s_1, s_2; s_1^*, s_2^*) = \{p[ps_1/(s_1 + s_1^*) + (1 - p)s_1/(s_1 + rs_2^*)] + \Delta r(1 - p)[(ps_2/(s_1^* + rs_2) + (1 - p)s_2/r(s_2 + s_2^*))]\}, \quad (3)$$

where Δ is the viability of eggs fertilized by males in role 2 (this is assumed to be one in role 1). Then the expected number of eggs fertilized by this male with a female if she copulates with this male and with an ESS male is

$$E'A(s_1, s_2; s_1^*, s_2^*) \quad (2a)$$

and each season the number of offspring per female that reach maturity is

$$GE'(A(s_1, s_2; s_1^*, s_2^*) + A(s_1^*, s_2^*; s_1, s_2)). \quad (2b)$$

To find ESS values for the numbers of sperm ejaculated, we consider first a mutant whose strategy is (s_1, s_2^*) , where $s_1 \neq s_1^*$. We suppose the mutant copulates n_1 times, each with a different female, and has energy resources R for reproduction. Then his "fitness", i.e. the number of offspring that survive to adulthood, is

$$W_m = GE' n_1 A(s_1, s_2^*; s_1^*, s_2^*),$$

in which s_2 in Eq. (3) becomes s_2^* . To find the ESS, W_m is maximized, subject to the energy constraint (Ball and Parker, 1997, 2000)

$$n_1(C + D(ps_1 + (1 - p)s_2^*)) = R, \quad (4)$$

where C is the energy used in finding a female, etc., and D is the energy used in producing one sperm. At the maximum we put $s_1 = s_1^*$. Using the method of Lagrange multipliers (Thomas and Finney, 1979) we get the following equations:

$$GE'(ps_1^*/(2s_1^*)^2 + (1 - p)rs_2^*/(s_1^* + rs_2^*)^2) - \lambda_1 D = 0, \quad (5)$$

$$GE' A(s_1^*, s_2^*; s_1^*, s_2^*) - \lambda_1(C + D[ps_1^* + (1 - p)s_2^*]) = 0, \quad (6)$$

where λ_1 is the Lagrange multiplier.

Consider a mutant male with strategy (s_1^*, s_2) and who copulates n_2 times. His fitness is $GE' n_2 A(s_1^*, s_2; s_1^*, s_2^*)$. With a similar constraint to Eq. (4), the equations are:

$$GE' \Delta r[ps_1^*/(s_1^* + rs_2)^2 + (1 - p)rs_2^*/(2rs_2^*)^2] - \lambda_2 D = 0, \quad (7)$$

$$GE' A(s_1^*, s_2^*; s_1^*, s_2^*) - \lambda_2(C + D[ps_1^* + (1 - p)s_2^*]) = 0. \quad (8)$$

Thus, from Eqs. (6) and (8), $\lambda_1 = \lambda_2$. Writing Eqs. (5) and (7) in terms of $z = s_1^*/rs_2^*$ we get an equation for Z :

$$f(z) \equiv \Delta r(1 - p)z^3 + [2\Delta r(1 + p) - p]z^2 + [\Delta r(1 - p) - 2(2 - p)]z - p = 0. \quad (9)$$

Substituting the result from this equation into Eqs. (5) and (6), we can obtain s_1^* and s_2^* .

There are some noteworthy mathematical points about Eq. (9): firstly it depends only on the product Δr

and not on the separate values; at $\Delta r = 1$, the solution is $z = 1$, and for $p = 0.5$, we have the solution $z = 1/r\Delta$, which implies $s_1/s_2 = 1/\Delta$. Thus in the random-roles model at $p = 0.5$, $s_1^* > s_2^*$; i.e. males ejaculate more sperm when in the favoured role 1. In Appendix A this is shown to be true for $p \geq 0.5$ and our calculations suggest it is true at all values of p . This result, $s_1^* > s_2^*$, contrasts with the solution for the game without sperm selection, where the ESS for the random-roles case is equal sperm expenditures in the two roles ($s_1^* = s_2^*$; Parker, 1990) unless sperm limitation is important (Mesterton-Gibbons, 1999a; Ball and Parker, 2000).

The female fitness, i.e. the number of offspring a female has, is (from Eq. (2b)),

$$2GE' A(s_1^*, s_2^*; s_1^*, s_2^*). \quad (10a)$$

The relative female fitness, i.e. relative to the maximum possible when $\Delta = 1.0$, $r^* = 1.0$, is

$$w_f = 2(E'/E)A(s_1^*, s_2^*; s_1^*, s_2^*). \quad (10b)$$

Both E' and A are functions of r , which evolution varies to maximize female fitness. Thus the local maximum with respect to variations in r is found when $A \, dE'/dr + E' \, dA/dr = 0$,

$$(11)$$

where, from Eq. (1),

$$A \, dE'/dr = 2cA(1 - r) \quad (12)$$

and, from Eq. (3),

$$E' \, dA/dr = -(1 - c(1 - r)^2)p(1 - p) \quad (1 - \Delta)s_1^*s_2^*/(s_1^* + rs_2^*)^2. \quad (13)$$

If this is not the global maximum, the latter may occur at the end points, $r = 0, 1$.

4. Analysis of the constant-types model

In this model, there are two different types of male, A and B. Type A occurs with frequency p , and ejaculates s_A sperm which is favoured by all females. Type B occurs with frequency $(1 - p)$, and ejaculates s_B sperm which is disadvantaged by all females. The ESS values of (s_A, s_B) are written (s_A^*, s_B^*) .

Consider the situation of a mutant A-type male, ejaculating s_A amount of sperm, while all the other males are in the appropriate ESS. His fitness is

$$n_A[p(s_A/(s_A + s_A^*)) + (1 - p)s_A/(s_A + rs_B^*)], \quad (14)$$

where he copulates n_A times. He is subject to the energy constraint

$$n_A[C + Ds_A] = R_A, \quad (15)$$

where we have assumed the costs C and D are the same for all males. To find the ESS values we maximize Eq. (14), setting $s_A = s_A^*$, subject to constraint (15). This

gives us the two equations:

$$p/4s_A^* + (1 - p)rs_B^*/(s_A^* + rs_B^*)^2 = \lambda_A D, \quad (16)$$

$$p/2 + (1 - p)rs_A^*/(s_A^* + rs_B^*) = \lambda_A(C_A + Ds_A^*). \quad (17)$$

We now consider a mutant B-male who ejaculates s_B sperm while all the other males play the appropriate ESS. His fitness is

$$n_B \Delta r [p(s_B/(s_A^* + rs_B)) + (1 - p)s_B/r(s_B + s_B^*)]. \quad (18)$$

We find the ESS as before, subject to the energy constraint

$$n_B[C + Ds_B] = R_B. \quad (19)$$

This gives the two equations:

$$\Delta [prs_A^*/(s_A^* + rs_B^*)^2 + (1 - p)/4s_B^*] = \lambda_B D, \quad (20)$$

$$\Delta [prs_B^*/(s_A^* + rs_B^*) + (1 - p)/2] = \lambda_B(C + Ds_B^*). \quad (21)$$

In general $\lambda_A \neq \lambda_B$. Writing $t \equiv rs_B^*/(s_A^* + rs_B^*)$ we get a quintic equation for t :

$$[p + 4(1 - p)t(1 - t)]t[1 - p + 4pt^2] = r[1 - p + 4pt(1 - t)](1 - t)[p + 4(1 - p)(1 - t)^2]. \quad (22)$$

Note that Eq. (22) does not explicitly depend on Δ . It varies with Δ , as r is determined by Δ through the effect of female preference. This is determined in the same way as in the random-roles model: the female's fitness is $2GE' A(s_A^*, s_A^*; s_B^*, s_B^*)$ and so the equations are the same with s_A^* replacing s_1^* , etc.

The equations for s_A^*, s_B^* reduce to the analogous equations obtained by Parker (1990) and Ball and Parker (2000) when female preference was not involved: for example when p is large and hence $1 - p$ is small we can neglect the matings of a female when two B males are involved, relative to those when one A- and one B-male are involved, and neglect the latter relative to the cases when two A-males are involved. Doing this we get $s_A^* = C/D$ and $s_B^* = Cs_A^*/Dr s_B^*$. Thus $s_B^* = C/D\sqrt{r} > s_A^*$, when $r < 1$. Similarly when p is small, we again get $s_B^* = C/D\sqrt{r} > s_A^* = C/D$, so that $s_B^* > s_A^*$ when $r < 1$.

When $p = 0.5$, Eq. (22) simplifies and becomes a cubic equation in t . This equation does not have an analytical solution, but has an approximate solution:

$$t \cong 0.5 - (1 - r)/[4(1 + r)]. \quad (23)$$

Using Eq. (23) we get

$$s_A^* = C/[D(1 + (1 - r)/(2(1 + r)))] \quad (24)$$

and

$$s_B^* = C/[D(1 - (1 - r)/(2(1 + r)))] \quad (25)$$

So that

$$s_A^* + s_B^* \cong 2C/D, \quad (26)$$

and again $s_B^* > s_A^*$.

In summary, at both limits for the frequency of A- and B-type males, and for the case where the frequencies of A and B are equal, the disfavoured male type ejaculates more sperm than the favoured male type, paralleling the result of Parker (1990) and Ball and Parker (2000). This conclusion was also supported at all frequencies of A and B used in the computations below.

5. Computations

Numerical solutions for the above equations in both models were derived as follows. For a given p, Δ , we assume a value of r : then we can calculate the ESS sperm amounts s^* , assuming that an ESS state occurs between the males. We can then calculate the derivative of the female's fitness for a given value of the cost parameter c . This is done for several values of r until the derivative is zero and fitness has a maximum; then r^* is a best reply to the male strategies. In certain circumstances female fitness is not maximized when the derivative is zero, in which case there is no ESS; this is discussed later. When it is, however, we have an ESS for both the males and the females.

6. Results

We first discuss the properties of the ESS for the two models in relation to Δ , the viability of offspring from the disfavoured male, for a population where favoured and disfavoured roles or types occur with equal probability ($p = 0.5$). Figs. 3 (for random roles) and 4 (for constant types) shows the ESS in relation to Δ both when the cost of sperm selection to the female (cf. Fig. 2) is relatively low ($c = 1/15$) and when it is relatively high ($c = 1/5$). In Figs. 3 and 4, it is convenient to consider the changes in a given ESS value (y -axis) as viability Δ (x -axis) decreases from its maximum value of 1.0 (i.e. from right to left).

6.1. Random-roles model

Fig. 3(a) shows the female's strategy at the ESS for random roles. As Δ decreases from 1, r initially decreases: the female biases paternity away from the disfavoured male by becoming more selective (i.e. by decreasing the value of r). This has the effect of decreasing the number of eggs she produces (Fig. 3(b)), i.e. it decreases E'/E , as she has to use up resources to reduce the value of r . However when Δ becomes much smaller, males should economize on sperm expenditure in the disfavoured role 2, s_2^* , to conserve sperm for matings in the favoured role 1 (Figs. 3(c) and (d) show the male's strategy in the two roles). Thus the female can here reduce her sperm selection costs, allowing r to

increase as Δ approaches 0 (Fig. 3(a)). In the appendix, we derive the behaviour of r, s_1^* and s_2^* as $\Delta \rightarrow 0$, confirming these ideas.

The behaviour of r as a function of Δ in the random-roles model is interesting: for a given value of p , with high sperm selection costs (e.g. Fig. 3(a); $c = 1/5$) r shows a minimum at an intermediate value for Δ . Because the cost of lowering r is high, the female can never approach total killing of the disfavoured ejaculate ($r \rightarrow 0$). However, for small sperm selection costs (e.g. Fig. 3(a); $c = 1/15$), we could not find solutions to the equations at certain intermediate values of Δ . This region is defined by the limits, Δ_0 and Δ_u , so that if $\Delta_0 < \Delta < \Delta_u$, we cannot find an ESS. We interpret this as follows: at low values of c , it would be in the female's interests to lower the value of r down to zero if this could generate an ESS in the male sperm allocation strategies. However if r is zero, a male should not ejaculate any sperm when in role 2, i.e. he should make $s_2^* = 0$. This in turn allows the female not to have to use resources to make r zero, as this would increase her costs unnecessarily. She can make r equal to 1 without loss due to Δ . Then males would make s_2^* non-zero, so that females should play $r \rightarrow 0$, and the argument goes on as before. Thus we conclude that in these circumstances there is no ESS for the combined system of males and females, and that strategies would change continuously, resembling the 'unresolvable evolutionary chases' found in sexual conflict over mating decisions (Parker, 1979).

The male's strategy in the two roles is shown for high costs of sperm selection in Fig 3(c) and low costs of sperm selection in Fig. 3(d). As expected, sperm expenditure in role 1 is greater than role 2 ($s_1^* > s_2^*$), but the behaviour of s_1^*, s_2^* in relation to Δ is complex. In the high costs case ($c = 1/5$), s_1^* initially increases as Δ declines from 1.0, reaches a peak, and then declines as Δ reduces further; s_2^* shows a sigmoidal decline as Δ declines from 1.0 to 0. In the low costs example ($c = 1/15$), s_1^* shows one peak in the region $\Delta_u < \Delta < 1.0$, and another in the region $0 < \Delta < \Delta_u$; s_2^* shows a sigmoidal decline across both regions as Δ decreases.

6.2. Constant-types model

Rather similar behaviour is seen in the constant-types model. At the ESS, the female continuously decreases r^* as Δ decreases from 1.0 (Fig. 4(a)). At values of $\Delta \leq \Delta_1$, where Δ_1 is a constant that depends on c and p , there is no ESS solution. The value of Δ_1 increases as sperm selection costs, c , to the female get smaller, i.e. as the female can affect disfavoured males' ejaculates more easily (compare curves for $c = 1/5$ and $1/15$). Unlike the random-roles model, there is no restoration of the ESS at low values of Δ . This is because males are of constant type, i.e. B males must expend sperm even though disfavoured: they have no option to economize on

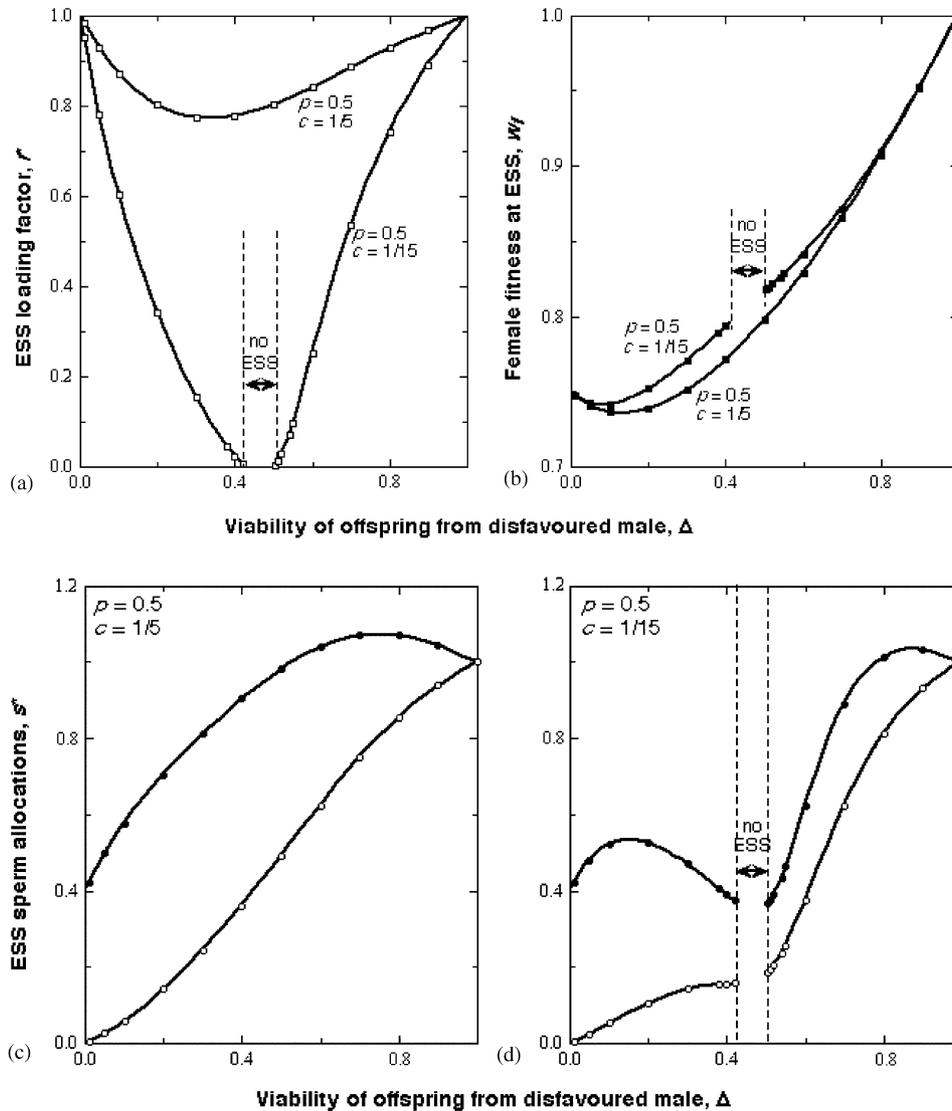


Fig. 3. Characteristics of the ESS for the random-roles model when favoured role 1 and disfavoured role 2 are equally probable ($p = 0.5$), in relation to Δ , the viability of offspring from disfavoured males. (a) ESS sperm selection, r^* , at two cost levels of sperm selection: $c = 1/5$ (high costs), and $c = 1/15$ (low costs) showing the region where no ESS exists. (b) Relative female fitness, w_f (see (10b)), for the same two cost levels. (c) ESS sperm allocations in role 1 (s_1^* ; filled circles) and role 2 (s_2^* ; open circles), when sperm selection costs are high ($c = 1/5$). (d) ESS sperm allocations in role 1 (s_1^* ; filled circles) and role 2 (s_2^* ; open circles), when sperm selection costs are low ($c = 1/15$) showing the region where no ESS exists.

sperm. Figs. 4(c) and (d) show ESS male sperm allocations for high ($c = 1/5$) and low ($c = 1/15$) sperm selection costs. As expected, favoured males expend less on their ejaculates than disfavoured males.

6.3. Effects of varying p , the frequency of the favoured role or type

Varying the proportion of favoured matings exerts a major effect on the ESS. As expected, the female's ESS for sperm selection, r^* , approaches 1.0 when $p \rightarrow 0$ or $p \rightarrow 1.0$: if only one sort of mating occurs, females have no choice of ejaculates and there is no point in paying

costs of sperm selection, which reaches a maximum (corresponding the minimum value for r) at intermediate frequencies. The case where $\Delta = 0.4$ (relatively high inviability of disfavoured ejaculates) and $c = 1/5$ (relatively high sperm selection costs to the female) is shown in Fig. 5: an ESS occurs across the entire range of p for both random-roles and constant types models. ESS sperm selection, r^* , reaches a minimum around $p = 0.4$, with the constant roles case showing the greater reduction in r .

The sperm allocation strategies at the same values for Δ and c are shown in Figs. 6(a) and (b). The ESS sperm allocations show very different patterns in the

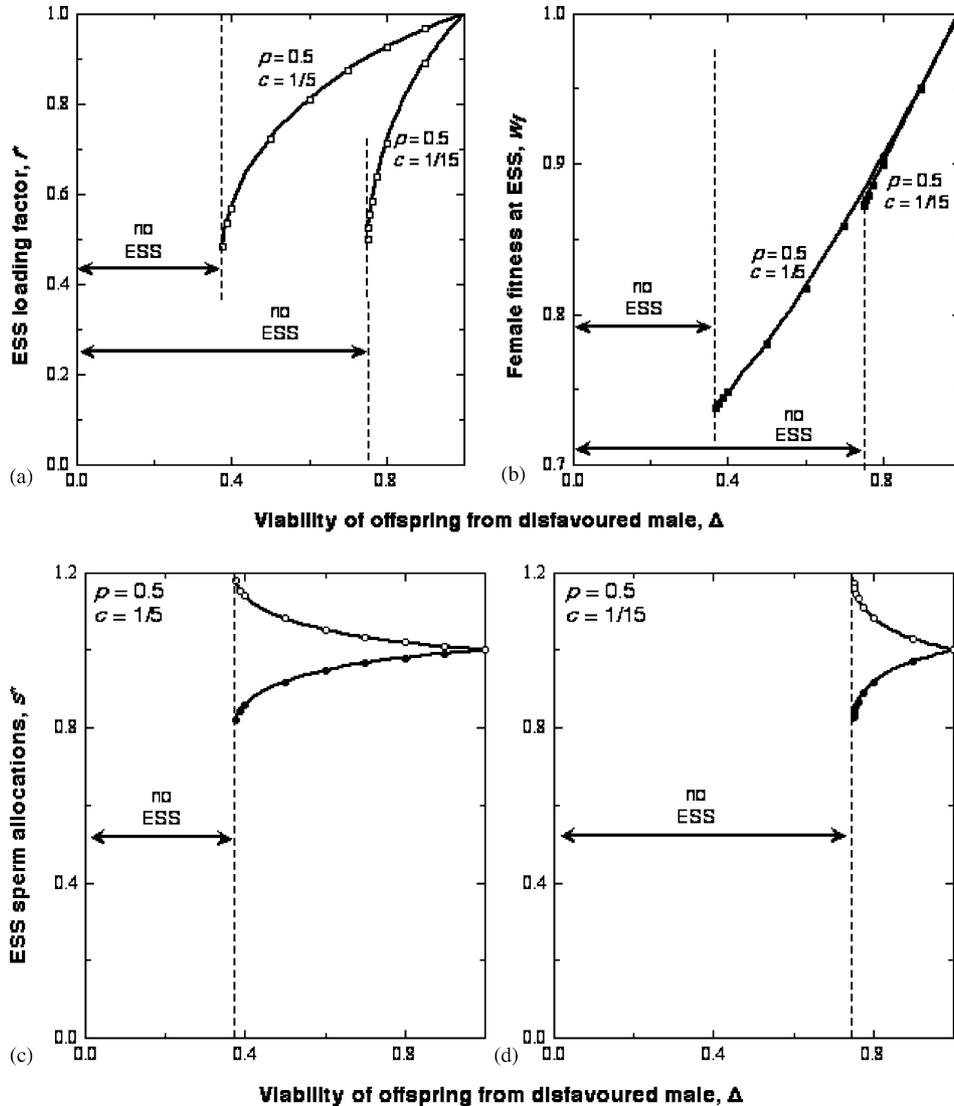


Fig. 4. Characteristics of the ESS for the constant-types model when males of favoured type A and disfavoured type B occur equally frequently in the population ($p = 0.5$), in relation to Δ , the viability of offspring from disfavoured males. (a) ESS sperm selection, r^* , at two cost levels of sperm selection: $c = 1/5$ (high costs) and $c = 1/15$ (low costs), showing the regions where no ESS exists. (b) Relative female fitness, w_f (see (10b)), for the same two cost levels. (c) ESS sperm allocations by A males (s_A^* ; filled circles) and B males (s_B^* ; open circles), when sperm selection costs are high ($c = 1/5$) showing the region where no ESS exists. (d) ESS sperm allocations by A males (s_A^* ; filled circles) and B males (s_B^* ; open circles), when sperm selection costs are low ($c = 1/15$) showing the region where no ESS exists.

random-roles and constant types models. In the random-roles case, the expenditure in the favoured role exceeds that in the disfavoured role across the entire range of p (Fig. 6(a)). In the constant types case, the expenditures at the limits, $p = 0, 1.0$, are equal; they diverge only between the limits, with greater expenditure by the disfavoured type (Fig. 6(b)).

The reason for the inequality of expenditures at the limits in the random-roles case relates only to the viability costs, Δ , that occur in the disfavoured role, and has nothing to do with sperm selection, since $r^* = 1.0$ at both limits. Provided that $\Delta < 1.0$, so that there are viability costs in role 2, it pays a male to conserve sperm

in the disfavoured role for expenditure in the favoured role, however often the roles occur. Thus if we set $r = 1.0$ in Eq. (9), we obtain

$$\frac{s_1^*}{s_2^*} = \frac{1 + 2\sqrt{\Delta}}{4\Delta - 1} \quad \text{for } p = 1.0$$

and

$$\frac{s_1^*}{s_2^*} = \frac{2}{\sqrt{\Delta}} - 1 \quad \text{for } p = 0.$$

Both the above equations have $s_1^* > s_2^*$ if $\Delta < 1.0$.

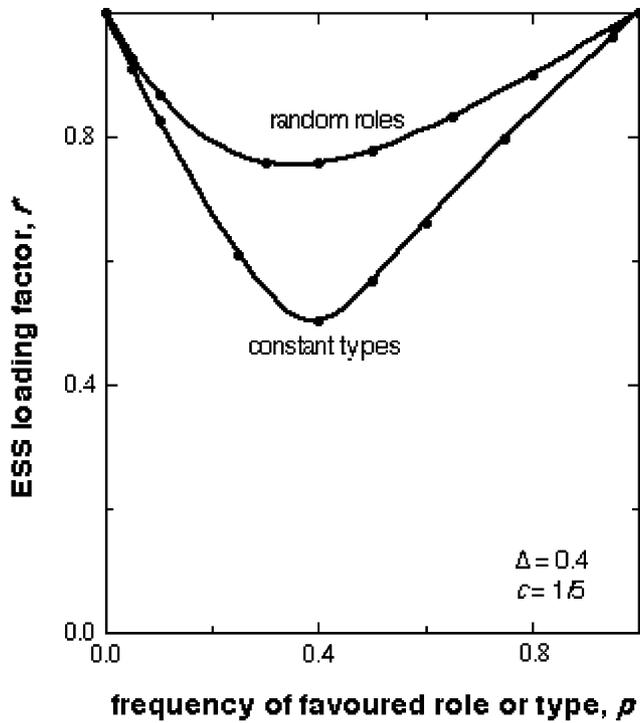


Fig. 5. ESS sperm selection, r^* , for the two models, when Δ (the viability of offspring from disfavoured males) = 0.4 and $c = 1/5$ (high sperm selection costs), in relation to p , the frequency of the favoured male role or type in the population. There is no region lacking an ESS under these conditions.

6.4. Incorporation of sperm limitation

A problem with the expressions that we have so far used, i.e. those of the pure raffle principle (Parker, 1990), is that sperm numbers are assumed to remain high enough to ensure complete fertilization even when the total amount $s^* \equiv s_1^* + rs_2^*$ of effective sperm is small or zero; this is when sperm limitation occurs. Mesterton-Gibbons (1999b) suggested that the proportion of fertilized eggs could be more accurately described by

$$s^*/(\varepsilon + s^*), \tag{27}$$

where ε is a constant. In most natural situations, ε is very small (Ball and Parker, 2000), so that the expressions we use are very close to this expression for most values of s^* .¹

However when r is comparable with ε , the differences between our expressions and those including sperm limitation are significant, and then sperm limitation must be taken into account. To include this effect in every term would make the algebra cumbersome and the resulting equations insoluble. We thus only include sperm limitation where it is necessary. In most of the terms of our expressions (see, for example, expression

¹Mathematically, the problem with an expression like $s_1^*/(s_1^* + rs_2^*)$ is that as $s^* \rightarrow 0$ it remains non-zero, whereas we would expect any sensible expression to go to zero continuously.

(3) for A), the difference between our formulae and those using the formula including sperm limitation are negligible. So in Eq. (3), sperm limitation is neglected in the first three terms because s_1^* (or s_A^*) is never small or comparable with ε , but the fourth term, $(1 - p)^2 \Delta rs_2/r(s_2 + s_2^*)$, needs to be replaced by

$$(1 - p)^2 \Delta rs_2/\varepsilon(s_2 + s_2^*), \tag{28}$$

particularly when r is small.

The equations for ESS sperm allocations for given r are no longer an equation in one variable, as in Eqs. (9) and (22), but now are two coupled polynomial equations in two unknowns, in both the random-roles and constant-types models. These can however be solved using numerical methods. We used values of ε equal to 0.001 in the random-roles model, and equal to 0.001 and 0.01 in the constant-types model.

Including this formulation of sperm limitation has the result that for the random-roles model, the region with no ESS no longer exists, i.e. where $\Delta_0 < \Delta < \Delta_u$. Instead, low values for r^* , s_1^* , s_2^* are generated in this region. For the other values of Δ , there is little difference between the values of r^* , s_1^* , s_2^* , in these calculations and the former ones. Fig. 7(a) shows how r^* changes with Δ when $\varepsilon = 0.001$, compared with $\varepsilon = 0$ (i.e. no sperm limitation). Other parameters were $C/D = 1.0$, $p = 0.5$ and $c = 1/25$. The rate of decline in r with Δ is very large at a particular value, written Δ_{lc} , of Δ , reminiscent of a phase transition (see Fig. 7(b)). The value of Δ_{lc} is almost the same as Δ_u .

The behaviour of the sperm numbers in this calculation ($C/D = 1.0$, $p = 0.5$, $c = 1/25$, $\varepsilon = 0.001$) is shown in Fig. 7(c): the values of s_1^* , s_2^* decrease considerably at $\Delta = \Delta_{lc}$, but for $\Delta < \Delta_{lc}$, they are continuous and finite, with no unusual behaviour, except that s_1^* increases slightly for $\Delta < \Delta_0$, and agree with our previous calculations. Thus males ejaculate a finite amount of sperm when in the disfavoured role in the region $\Delta_0 < \Delta < \Delta_u$, and thus females cannot raise their r -values to one.

In the calculations without sperm limitation, the ratio C/D , i.e. the amount of energy spent by a male on finding a female relative to ejaculating a unit amount of sperm, does not affect the value of r^* . The values of s_1^* , s_2^* are also linearly proportional to C/D , so that the amount of energy spent by a male on finding a female relative to the amount spent on ejaculation is independent of C/D . However, in calculations with sperm limitation, the ratio C/D changes both the amount a male expends on finding a female, etc., relative to the amount spent on ejaculation, and the values of r^* . We made calculations for various values of C with D fixed at 1.0. The values of r^* in those regions where there was originally no ESS became smaller as C increased. We thus conclude that the fact that the original model for random roles gave no ESS is just an artefact of the

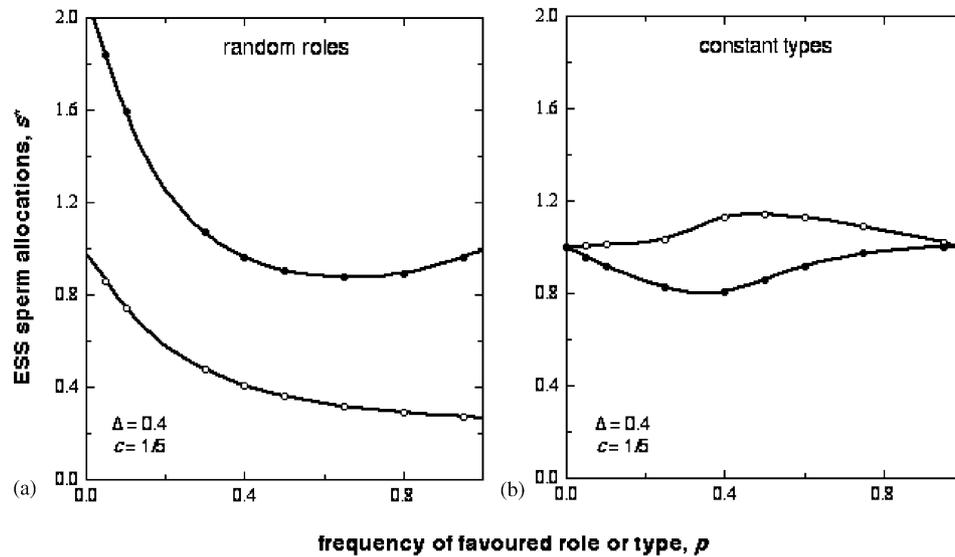


Fig. 6. ESS sperm allocations for the two models, when Δ (the viability of offspring from disfavoured males) = 0.4 and $c = 1/5$ (high sperm selection costs), in relation to p , the frequency of the favoured male role or type in the population. There is no region lacking an ESS under these conditions. (a) Allocations in the random-role model in role 1 (s_1^* ; filled circles) and role 2 (s_2^* ; open circles). (b) Allocations in the constant-types model by A males (s_A^* ; filled circles) and B males (s_B^* ; open circles).

model: what actually happens is that in the region $\Delta_0 < \Delta < \Delta_u$, r^* is small and the ejaculates, s_1^*, s_2^* , are finite.

In contrast with these results, including sperm limitation causes negligible changes in the “constant-type” model: the regions where the ESS does not occur (i.e. where $\Delta < \Delta_l$) remain as before. Increasing the value of ε by a factor of 10 (to 0.01) altered the results only marginally, and did not change their nature. We thus conclude that the absence of an ESS in this region is a real effect.

The reason why incorporation of sperm limitation changes the nature of the results is that the term (28) is a constant when sperm limitation is ignored. Then the female can make r small without seriously affecting her fertility if the costs of changing r are small. However, when sperm limitation is incorporated, this term becomes very small for r small, and she may thus suffer a large reduction in fertility. We note that in the random-roles model, this occurs at largish values of Δ , whereas in the constant-types model, the no-ESS effect occurs at small values. Thus, in the latter, the changes in the term (28) are not so significant, and sperm limitation does not have any effect.

Though we have not investigated this analytically, the region of no ESS may be stabilized in both models by application of the ‘trembling hand’ principle in game theory (Selten, 1975; Osborne and Rubinstein, 1999): strategies can be seen as choices of the costs of each investment in sperm allocation or sperm selection, but the levels of these actually realized are distributed around their mean values, due to some random variable

(e.g. chance variations in an individual’s condition and investment capacity). Such random variations in realized strategies as proposed by Selten can stabilize evolutionary games (e.g. Parker, 1983). We would expect ESS sperm selection to stabilize at some high level (i.e. low r^*) in such regions, rather as with sperm limitation in the random-roles model.

7. Biological discussion

7.1. Overview and synthesis of results

This paper complements previous studies of sperm competition games, all of which have examined the evolution of sperm expenditure under sperm competition, but with no strategic influence by the female on male strategies (for a review of earlier work see Parker, 1998, 2000; and subsequently Mesterton-Gibbons 1999a, b; Fryer et al., 1999; Ball and Parker, 1998, 2000; Greef and Parker, 2000; Greef et al., 2001). In our present analysis, males compete for fertilizations by sperm competition (Parker, 1970) and females can operate sperm selection against unfavourable ejaculates by cryptic female choice (Thornhill and Alcock, 1983; Eberhard, 1996). Both sexes can respond strategically to the other: over evolutionary time sperm allocations are regulated depending on whether males are favoured or disfavoured by given females, and female’s levels of sperm selection against unfavourable ejaculates are changed. Both strategies, sperm expenditure and investment on sperm selection, are constrained by trade-offs:

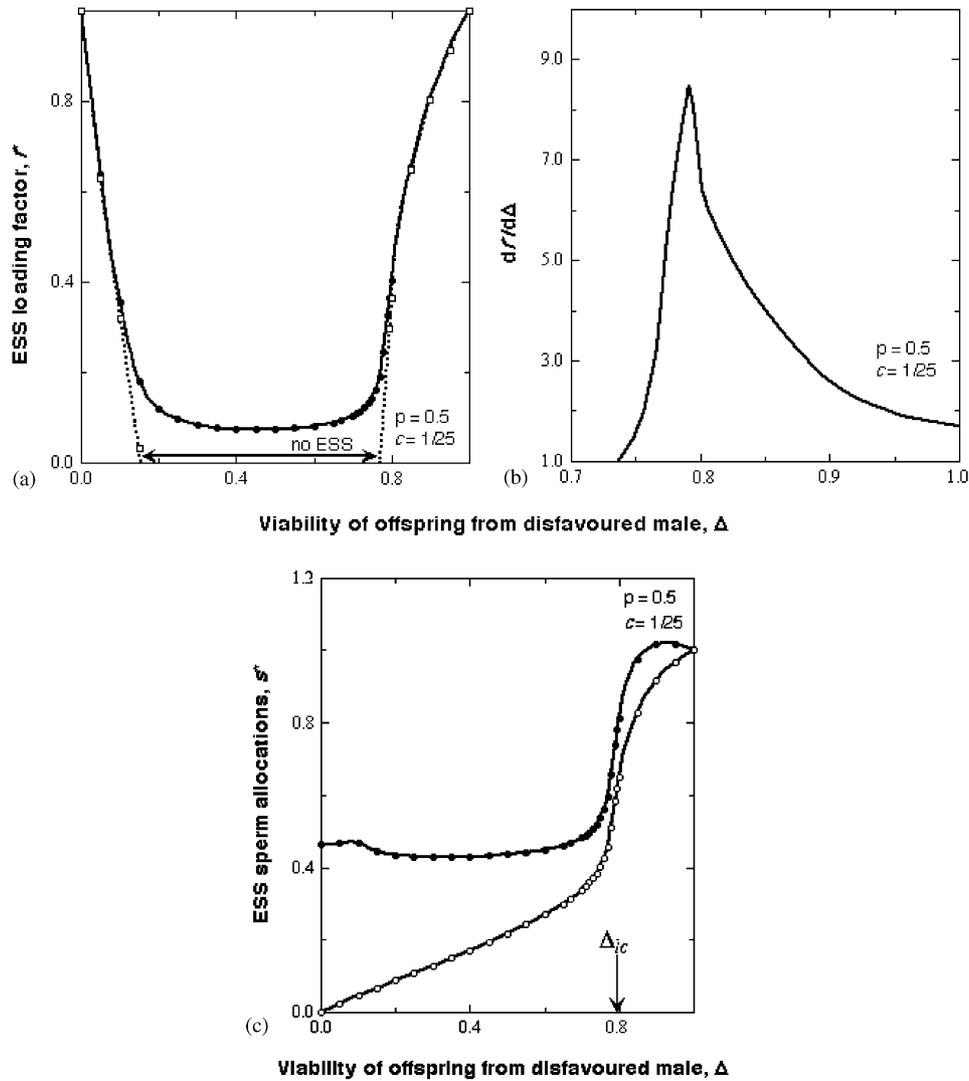


Fig. 7. Effect of sperm limitation in the random-roles model, when the favoured role 1 and disfavoured role 2 are equally probable ($p = 0.5$), sperm selection costs are very low ($c = 1/25$) and $C/D = 1.0$. (a) ESS sperm selection, r^* , for the random-roles model, in relation to Δ (the viability of offspring from disfavoured males). The dotted (squares) line shows the result for the basic model (i.e. no sperm limitation; $\varepsilon = 0$), with a no ESS region between $\Delta_0 \approx 0.15$ and $\Delta_u \approx 0.77$. The continuous line (filled circles) shows the result when sperm limitation is included with $\varepsilon = 0.001$, which generates an ESS across this region. (b) The rate of change of sperm selection with the viability of offspring from disfavoured males, $dr^*/d\Delta$, in relation to Δ . We find $\Delta_{lc} \approx 0.79$. (c) ESS sperm allocations in role 1 (s_1^* ; filled circles) and role 2 (s_2^* ; open circles) in relation to Δ .

males trade off sperm against mate searching or other mate-acquiring activity, and females trade off sperm selection against fecundity. For males, increasing sperm expenditure increases paternity under sperm competition, and for females, since disfavoured males have less viable offspring than favoured males, sperm selection increases the number of surviving young.

We have shown that resolution of this form of game depends critically on whether males are equal, and are favoured or disfavoured by different subsets of the female population (random-roles) model, or unequal, so that given males are either favoured or disfavoured by all females (constant-types model). This distinction was

made in the first sperm competition game analysis (Parker, 1990) in relation to cases where 'favoured' and 'disfavoured' reflected fixed aspects of what happened in the female (e.g. differential fertilization success due to mating order: first to mate, second to mate). The distinction between 'roles' (the various circumstances males face due to what happens in females) and 'types' (the male's phenotype) was clarified more recently due to analyses by Mesterton-Gibbons (1999a) and Ball and Parker (2000). In the random-roles model, roles and types are uncorrelated and we seek the ESS assuming all males to be equal (which, on average, they are with respect to role). In the constant-types model, roles are

Table 1
Summary of predictions for the random-roles model

Player	General prediction	Effect of viability (Δ) of progeny of disfavoured male	Effect of cost (c) of sperm selection to female	Effect of frequency (p) of favoured role
Female	Sperm selection against males in disfavoured role	Maximum sperm selection at intermediate Δ values (relation can be complex)	Sperm selection increases as cost c reduces—without sperm limitation, the ESS can be lost if c is low	Maximum sperm selection at intermediate p ; no sperm selection at limits ($p = 1, 0$)
Male: Favoured role 1	Higher sperm allocation	Maximum sperm expenditure at relatively high (not maximum) Δ (relation can be complex)	Expenditure tends to reduce with c	Relation complex: sperm expenditure higher than disfavoured role even at limits ($p = 1, 0$)
Male: Disfavoured role 2	Lower sperm allocation	Maximum sperm expenditure at maximum Δ (relation can be complex)	Expenditure tends to reduce with c	Relation complex: sperm expenditure lower than favoured role even at limits ($p = 1, 0$)

Table 2
Summary of predictions for the constant-types model

Player	General prediction	Effect of viability (Δ) of progeny of disfavoured male	Effect of cost (c) of sperm selection to female	Effect of frequency (p) of favoured male type
Female	Sperm selection against males in disfavoured role	Sperm selection increases as Δ decreases, to the region of no ESS, which applies for all $\Delta < \Delta_1$	In ESS region, sperm selection increases as cost c reduces—ESS threshold Δ_1 increases as c decreases	Maximum sperm selection at intermediate p ; no sperm selection at limits ($p = 1, 0$)
Male A: Favoured type	Lower sperm allocation	Sperm expenditure decreases as Δ decreases from 1.0 to the region of no ESS $< \Delta_1$	In ESS region, expenditure decreases as c reduces	Minimum sperm expenditure at intermediate p ; expenditure lower than disfavoured role except at limits ($p = 1, 0$)
Male B: Disfavoured type	Higher sperm allocation	Sperm expenditure increases as Δ decreases from 1.0 to the region of no ESS $< \Delta_1$	In ESS region, expenditure increases as c reduces	Maximum sperm expenditure at intermediate p ; expenditure higher than favoured role except at limits ($p = 1, 0$)

exactly correlated with type, and we seek an ESS conditional on a male's phenotype (which specifies the role he will always occupy).

The main predictions of the models are summarized in Tables 1 and 2 (random roles) and (constant types). Both models can generate ESS solutions, and the random-roles model always appears to generate an ESS when sperm limitation is included. The conclusions about strategies are:

- (i) *Sperm selection*: At the ESS, females show sperm selection for all cases where the males differ in the viability of their progeny. Sperm selection increases as its associated costs decrease, and increases as the difference between males increases. In the random-roles model, if sperm selection is costly, sperm selection reaches a maximum across an intermediate region of viability, but then decreases again as the viability level decreases towards zero (where the ESS sperm selection becomes zero). If sperm selection is uncostly, this region of intermediate

viability has an ESS only if the effects of sperm limitation (i.e. some eggs fail to be fertilized because sperm numbers are too low) are included; then there is high sperm selection across the region. This U-shaped relation for r^* (Figs. 3(a) and 7(a)), with sperm selection decreasing at both ends of the viability range, occurs because under low viabilities, it pays males to conserve sperm for matings in the favoured role where their offspring will have high viability, thus allowing females to relax sperm selection. In the constant-types model, there is no region where sperm selection decreases as progeny viability becomes low (Fig. 4(a)): as viability decreases from 1.0, sperm selection increases monotonically. If sperm selection is costly, this decrease may continue across the most of the range of progeny viability, depending on the frequencies of the two types. But if sperm selection is uncostly, there is a region of lowest viability where there is no ESS, and unlike the random-roles model, this cannot be stabilized by including sperm limitation.

Disfavoured males in the constant-types model are always disfavoured, and hence cannot conserve sperm for alternative, more favourable, sources of mating. In the ESS region, sperm selection increases as its associated costs decrease, and the threshold viability level below which there is no ESS increases as costs decrease. Maximum sperm selection appears to occur at intermediate frequencies of the favoured male role or type in both models (Fig. 5), but to a greater extent in the constant-types model. There is no sperm selection at the frequency limits.

- (ii) *Sperm allocations*: With random roles, males always allocate more sperm when occupying the favoured role, whatever the frequencies of the two roles (Fig. 6), though the relation between the ESS allocation and progeny viability can be complex (e.g. Figs. 3(d) and 7(a)). Maximum sperm expenditure in the favoured role occurs at high, but not maximum progeny viability, whereas in the disfavoured role, maximum expenditure occurs at maximum viability ($\Delta = 1.0$). Expenditure tends to reduce as sperm selection costs reduce, i.e. as sperm selection by the female increases (Figs. 3(c) and (d)). This matches earlier predictions for random-roles models that overall sperm expenditure decreases as the loading in the raffle increases (Parker et al., 1997). With constant types, the favoured male type allocates less sperm than the disfavoured type, unless one or other type is extremely rare, when expenditures become equal (Fig. 6). In the ESS region, sperm expenditure of favoured males decreases as viability of progeny of disfavoured males decreases from 1.0 to the region of no ESS, i.e. $0 \leq \Delta \leq \Delta_l$ (Figs. 3(c) and (d)), but sperm expenditure of disfavoured males increases as Δ decreases from 1.0 to Δ_l (Figs. 4(c) and (d)). Expenditure of favoured males decreases as c reduces (Figs. 3(c) and (d)), but expenditure of disfavoured males increases as c reduces (Figs. 4(c) and (d)).

Note that males also feel the cost of inviability. For the random-roles model, this creates for males two female categories, good and bad, exactly as there are good and bad males from the female perspective. For the constant-types model, different viabilities of offspring for the two males affect male strategy only via the effect of the female's response; disfavoured males have no better option for which to conserve sperm. This crucial difference between the two models generates the very different predictions.

Thus the predictions for the two models differ considerably, as in earlier models where the raffle loading was fixed, rather than under the strategic control of the female. It is therefore important that empiricists studying cryptic female choice and sperm

allocation patterns determine whether sperm selection is applied differently, or consistently, on given males by different females in the same population.

7.2. Sperm selection and sperm selection costs

Experimentally, it is rather difficult to demonstrate sperm selection with certainty (e.g. Birkhead, 1998; Simmons and Siva-jothy, 1998; Telford and Jennions, 1998; Simmons, 2001); differential paternity among males is insufficient alone since many other possibilities must be discounted. For example, unequal paternity can arise as a purely male effect. For example, in yellow dungflies, *Scatophaga stercoraria*, larger males transfer sperm at a faster rate, so that if two competing males are allowed a fixed mating time, the larger male will have higher paternity because they have more sperm in the female's sperm store when competing against a smaller male (see Simmons, 2001). Also, males may be expected to transfer more sperm when the benefits are potentially higher, and there is some evidence for this (dungfly males ejaculate more sperm when mating with females that contain more eggs) (Parker et al., 1999). However, there is a growing body of evidence for sperm selection (see e.g. Jennions and Petrie, 2000; Simmons, 2001), and it has been in response to this that the present models have been devised.

Biologically, it is not yet clear what are the costs of sperm selection; this forms an important part of the present models. When females have more than one sperm storage organ (as applies in many insects), they may be able to store different ejaculates in different organs, and hence regulate paternity (Hellriegel and Ward, 1998). Sperm selection costs would here relate to the costs of the structures and mechanisms necessary to operate them. In organisms which lack this capacity, sperm selection is more likely to be achieved by molecular mechanisms related to immunological recognition of unfavourable sperm, and the costs of sperm selection may be the expenditure on immunologically active cells in the female tract, or to recognition mechanisms acting at the time of fertilization. Such processes are still uncertain, and empirical validation of the assumptions of the models remains unavailable.

The notion that males may compete for fertilizations if their prospects are zero (e.g. males in role 2 or *B* phenotypes when disfavoured male's have progeny viability $\Delta = 0$) is untenable. This is not a difficulty in the random-roles model since in this situation males in role 2 allocate zero sperm (effectively they do not mate). But in the constant-types model the case where $\Delta \rightarrow 0$ is biologically unrealistic, because genes that create such males are lost from the population each generation. It is plausible that 'poor quality males' may have Δ at some intermediate value, but not approaching zero.

7.3. The biological rationale for the two model approaches

Why model random roles and constant types? This approach began with the early models (Parker 1990), and was chosen to represent two ends of a continuum. At one extreme, the different circumstances faced by ejaculates within the female tract (i.e. roles) occur randomly to particular males, so that each male faces mixed opportunities. At the other extreme, a particular male is characterized by a particular role faced by its ejaculate. There is obviously much variation between these extremes and recent research (Mesterton-Gibbons, 1999b; Ball and Parker, 2000) has focussed on how sperm allocations will vary when males occupy roles non-randomly, but not constantly.

In the context of the present paper, for constant types we envisage a population in which there are 'good' and 'bad' male genotypes, so that 'bad' males have less viable offspring. This is a simplification of one of a set of classical assumptions made for precopulatory female choice in sexual selection (see Andersson, 1994). Much discussion has related to the maintenance of the genetic variation (what maintains bad genotypes) under such choice, and explaining the maintenance of the genetic variation that forms the basis of the choice (see Andersson, 1994). Exactly the same problems beset postcopulatory female choice by sperm selection.

In contrast, the random-roles approach assumes males are similar in fitness overall, but not equally successful with all females. Some recent studies of sperm selection support the view that females select sperm on a basis of genetic compatibility, where incompatible genetic combinations can result in embryonic inviability (e.g. Bishop (1996), Bishop et al. (1996), Zeh and Zeh (1996, 1997), Tregenza and Wedell (2000); for review of possible processes see Simmons (2001)). We had this sort of process in mind when devising the random-roles model.

One special case where genetic incompatibility and random roles may apply is in matings between related individuals. There is evidence that females may use sperm from unrelated males preferentially when unrelated ejaculates are in competition with sperm from brothers (Wilson et al., 1997; Stockley, 1999; Tregenza and Wedell, 2000, 2002). However, our present models are not adequate to cover such situations; matings between related individuals would require an inclusive fitness approach.

Sperm selection involving two intermixing species, I and J, represents an extension and amalgamation of both random-roles and constant-types models, because although there are two distinct phenotypes of both males and females, individuals of a given sex and species meet both partner options, I and J, randomly. Thus instead of having a single population with two

sperm selection roles, we would need to include in the model the frequencies with which I and J species meet, in all combinations of sexes, which greatly complicates the analysis. Data on sperm competition between the same and closely related species usually results in conspecific sperm precedence (for recent reviews, see Howard, 1999; Simmons, 2001), i.e. a bias favouring conspecific progeny at fertilization in competition with heterospecific sperm. This bias is often incomplete, and overlies the basic pattern of sperm utilization. For most species, the mechanism is not known and may reflect a number of possibilities, e.g. different sperm allocations, reduced survival or competitiveness of the heterospecific sperm in the foreign female tract, differential resistance of eggs against sperm penetration, etc. However, in some instances it appears that there is differential selection against heterospecific sperm. For instance, in ladybird beetles, *Epilachna vigintioctomaculata* and *E. pustulosa*, heterospecific sperm seem to be incapacitated in the female tract (Katakura, 1986). A similar situation may apply in the ground crickets, *Allenobius fasciatus* and *A. socius* (Gregory and Howard, 1994). Within each species, there is storage of sperm from multiple males and mixed paternity. But sperm competition involving hetero- and conspecific ejaculates resulted in very strong bias towards fertilization by conspecific sperm, though increasing the proportion of heterospecific sperm present reduced or offset this advantage to conspecific males (Howard and Gregory, 1993), as in the assumptions of the present models.

A number of studies show that females mating multiply produce more surviving offspring than those mating singly (e.g. Madsen et al., 1992; Zeh and Zeh, 1997; Tregenza and Wedell, 1998; Watson, 1998). This may be interpreted in several ways, one of which is that males vary in their sire quality from the female perspective and that the female can select among sperm. If this is the reason, the process could fit either random-roles or constant-types models depending on whether given males are universally poor or whether the difference relates to genetic compatibility. However, there are other interpretations of such results and a recent study by Simmons (2001) found no viability differences between males who were successful in such competitions and those who were not.

The study of the theory of sperm selection is in its infancy, and our present models represent a prospective attempt to formulate an approach to the logic of such processes.

Acknowledgements

We thank Dr. Tom Pizzari for comments that have helped to improve the manuscript.

Appendix A

Proof that $s_A^* > s_B^*$ in the random-roles model, for $p \geq 0.5$.

The function $f(z)$ is a cubic equation in z such that as $z \rightarrow \pm \infty$, $f(z) \rightarrow \pm \infty$, respectively, because the coefficient of z^3 is always positive. At $z = 0$, $f(0) < 0$, and the derivative $f'(0) < 0$. Thus there is a turning point of $f(z)$ at $z < 0$, and hence there can only be one solution of $f(z) = 0$ in the region $z > 0$, the only region of interest.

Now

$$f(1/r\Delta) = (1 - 2p)(1/r\Delta - 1)^2, \quad (\text{A.1})$$

so that at $z = 1/r\Delta$, $f < 0$ when $p > 0.5$. Thus the zero of f occurs for a value of $z > 1/r\Delta$ for such values of p so that

$$s_1^*/s_2^* > 1/\Delta \text{ implying } s_1^* > s_2^*.$$

Note that the above shows that f has a zero when $p = 0.5$.

We have not been able to prove the result for $p < 0.5$, but our calculations suggest that it is so.

Appendix B

Behaviour of r, s_A^* , etc., as $\Delta \rightarrow 0$ in the random-roles model.

We only consider the situation where sperm limitation is neglected. Except where there is no ESS this is sensible in all situations for $\Delta > \varepsilon$. The mathematics when sperm limitation is included is different from this for $\Delta < \varepsilon$, but as this is of little biological interest, we do not consider it here.

As A, E', D and λ are finite, we see from Eqs. (5) and (7) that as $\Delta \rightarrow 0$, s_1^* is finite, $s_2^* \rightarrow 0$, but Δ/s_2^* is non-zero. Thus from the Eq. (11) for maximization of the female fitness, that $A \, dE'/dr = 0$, which implies that $r \rightarrow 1$. Thus, for Δ small, we write $s_1^* = a + b_1\Delta$, $s_2^* = b_2\Delta$, $r = 1 - b_2\Delta$, where a, b_1, b_2, b_3 are all dependent only on p and possibly c . Equations for the coefficients a, b_1, b_2, b_3 can be obtained for general p but they are complicated. Here we present the results for the case $p = 0.5$. Then, as $s_1^*/s_2^* = 1/\Delta$,

$$b_2 = a. \quad (\text{B.1})$$

We also get

$$a = 2C/5D \quad (\text{B.2})$$

which, when $C = D = 1$, gives $a = 0.4$. Our results agree with this. The other results are:

$$b_1 = 3a[2 + Da]/[2C - Da], \quad (\text{B.3})$$

$$b_3 = 1/3c. \quad (\text{B.4})$$

Our calculations are in agreement with these analytic results.

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