On sperm competition games: incomplete fertilization risk and the equity paradox

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Evolutionary game theory has been used to predict the effect on sperm expenditure of a trade-off between the value of a mating and the cost of its acquisition. In particular, G. A. Parker has predicted that, if two males 'know' whether they are first or second to mate, but these roles are assigned randomly, then sperm numbers should be the same for both males whether the 'raffle' for fertilization is fair or unfair. This prediction relies on the assumption that, in the absence of sperm competition, ejaculates would always contain enough sperm to ensure complete fertilization after mating. The slightest risk of incomplete fertilization, however, is enough to ensure that favoured males expend more than disfavoured males in the presence of sperm competition, unless the competition is perfectly fair. Divergence of expenditures increases with unfairness until unfairness reaches a critical value, beyond which a disfavoured male should no longer compete. The higher the fertilization risk, the lower the critical unfairness. All predictions are independent of the probability of mating first or second. Implications are discussed for the mechanisms that underlie sperm competition.

Keywords: evolutionarily stable strategies; game theory; sperm competition

1. INTRODUCTION

Sperm competition is competition between the ejaculates of different males for fertilization of a given set of eggs. For example, male 13-lined ground squirrels, *Spermophilus tridecemlineatus*, routinely 'queue' for mating with oestrous females, typically in pairs, with the first male having an advantage (Schwagmeyer & Parker 1990, 1994). Ejaculates are expensive, in the sense that increased expenditure of reproductive effort on a given ejaculate reduces the number of matings that can be achieved, and evolutionary game theory has been used to predict how this trade-off affects sperm expenditure (Birkhead & Parker 1997). In principle, there are two approaches to modelling the trade-off: after suitably defining mating value in the absence of any trade-off, one can either multiply that value by an appropriate discount or subtract an appropriate cost. I refer to the first of these approaches as multiplicative and to the second as additive. Recently (Mesterton-Gibbons 1999), I compared them in the context of Parker (1990), who adopted the multiplicative approach. I found that, although results were similar in many respects, and sometimes even identical, the multiplicative approach was inconsistent with Parker's (1990) assumption that the cost of mating increases with sperm expenditure but does not depend on the role in which sperm is expended. As a consequence, Parker's analysis allowed evolutionarily stable sperm expenditures in given roles to depend on the probabilities of occupying those roles, even though animals had full information about them. By contrast, the additive approach maintained the independence of the full-information evolutionarily stable strategy (ESS) from the probabilities of role occupation. Thus the

additive approach is more fundamentally correct, and here I adopt it exclusively.

Parker's analysis of sperm competition yielded two results that he found paradoxical. The first was that, if males 'know' whether they are first or second to mate, but these roles are assigned randomly, then sperm numbers should be equal for the two males whether the 'raffle' for fertilization is fair or unfair. The second result was that, if mating order is non-random, then the favoured male should expend less on sperm. Despite the paradox, Parker extrapolated from his second result to offer two qualitative conclusions, namely, '(i) if a male occurs more often in the disfavoured role, his sperm expenditure is likely to be greater than if he occurs more often in the favoured role; (ii) favoured males will spend less on sperm, and disfavoured males more, as the degree of unfairness increases.'

Parker's two results were puzzling not only in terms of intuition about nature, but also in terms of his model's consistency. In other words, they presented both an external paradox and an internal paradox. Mesterton-Gibbons (1999) has shown that the paradox of random roles can be internally rationalized in terms of standard microeconomic theory, and that the constant-role paradox is merely an artefact of the multiplicative approach. Thus neither of Parker's (1990) qualitative conclusions from his constant-role model should necessarily hold. Nevertheless, there remains the external paradox of equal expenditure when roles are randomly assigned, and in this article I address it.

In general, the only way to resolve a paradox is to spot the false assumption that generated it (Mesterton-Gibbons & Adams 1998). So if Parker's (1990) prediction of equal expenditures seems paradoxical, then what does his model assume, perhaps implicitly, that nature contradicts? A

possible answer is symmetry of costs: if the costs of sperm expenditure at a second mating are not the same as at a first mating, then sperm expenditure at the ESS will be higher in the cheaper role. As Parker (1990) pointed out, however, cost symmetry is a perfectly reasonable assumption for a vertebrate in which the male performs no parental care or guarding, thus allocating reproductive effort between sperm production and mate acquisition. So this possible answer seems unlikely to be correct in general. A second possible answer was suggested by Mesterton-Gibbons (1999), who conjectured that the fairness of the fertilization raffle to a disfavoured second male is not constant, as Parker (1990) assumed, but decreases with the amount of sperm expended by the favoured first male: then sperm expenditure by the second male will always be lower at the ESS. Nevertheless, the physiological mechanisms that might support this conjecture are largely unexplored (Birkhead & Parker 1997).

Accordingly, in this paper I explore a third possibility. Let r denote Parker's (1990) loading factor, i.e., the effectiveness ratio of a unit of disfavoured sperm compared to a unit of favoured sperm: as r increases from 0 to 1, the unfairness of the favoured male's advantage in the 'raffle' for fertilization decreases, until the raffle becomes fair when $r = 1$. As remarked above, Parker's (1990) model predicts that a disfavoured male's sperm expenditure at the ESS, say σ (see §3), is equal to that of a favoured male for any value of r , and that σ increases with r . Parker's model also predicts, however, that $\sigma \rightarrow 0$ as $r \rightarrow 0$, or that sperm expenditure is virtually zero when the raffle is extremely unfair. Thus Parker's prediction of equal expenditures at all values of r relies, at least in part, on his assumption that ejaculates would always contain enough sperm to ensure complete fertilization after mating in the absence of any sperm competition; in other words, that there is no sperm limitation. This assumption clearly cannot hold as sperm expenditure approaches zero: then nature contradicts what the model assumes. In any event, there is now considerable evidence that sperm limitation may be widespread in nature, at least where fertilization is external; see, for example, Levitan & Petersen (1995), Lasker *et al.* (1996) and Shapiro & Giraldeau (1996).

Throughout, I follow Parker (1990) in defining sperm expenditure to mean number of sperm released per ejaculate. Other, less narrow, definitions of sperm expenditure are commonly used in empirical studies and are necessary for several reasons, perhaps the simplest being that animals may vary energetic expenditure per ejaculate by varying sperm size as well as sperm number (Parker 1993). Nevertheless, the definition I adopt is the most expedient to my purpose, namely, to explore the effect on sperm competition of incomplete fertilization risk, and in particular to determine whether it can resolve the random-role paradox. To that end, I exclude various other effects on sperm competition that Parker and his collaborators have already modelled, the most recent example being the effect of risk assessment (Parker *et al.* 1997). For reviews of these developments, see Parker (1998) and Parker & Ball (1999).

2. MATHEMATICAL MODEL

Consider a game among a population of males who mate randomly either with unmated or with once-mated

females from a population of females who always mate exactly twice. The proportion of unmated individuals among the female population may be any positive number less than unity. Thus each male may occupy either of two roles, and a strategy consists of an amount of sperm to ejaculate in each. Unless the raffle is fair, one of these roles is favoured; I denote it by A, and the disfavoured role by B. Let the amounts ejaculated in roles A and B be v_1 and v_2 , respectively, for the population strategy but u_1 , u_2 for a mutant. That is, a mutant's strategy is a two-dimensional vector $u = (u_1, u_2)$ in which u_1 is the amount of sperm ejaculated when that male is in role A, and u_2 is the amount of sperm ejaculated when he is in role B. Similarly, the population strategy is $v = (v_1, v_2)$, where v_1 and v_2 are the amounts of sperm ejaculated in roles A and B, respectively.

For any given female, let K denote her maximum potential future reproductive success from a given set of eggs, let X denote the favoured male's sperm expenditure, let Y denote the disfavoured male's expenditure and let T ($\leq X + Y$) denote the female's effective total number of sperm. To obtain T , one devalues the disfavoured male's expenditure by the loading factor r . That is,

$$T = X + rY. \quad (1)$$

Let $Kg(T)$ denote the female's expected future reproductive success as a function of effective total sperm number. The proportion g is a concave increasing function of T , with $g(0) = 0$ and $g(\infty) = 1$; see, for example, fig. 1 of Warner *et al.* (1995, p. 136). For the sake of simplicity, I assume a Michaelis-Menten dependence of the form

$$g(T) = \frac{T}{\epsilon + T}, \quad (2)$$

except where otherwise indicated. Here ϵ is the number of sperm that would fertilize half of a female's eggs. There is empirical support for equation (2) in the literature; for example, with $\epsilon = 0.117$ it yields a good approximation to the data of Warner *et al.* (1995) on proportion of eggs fertilized versus (millions of) sperm per spawn in the bluehead wrasse, *Thalassoma bifasciatum*. I assume throughout that ϵ is relatively small, in a sense made precise by inequality (7) below. Note that Parker (1990) in effect assumed $\epsilon = 0$.

Reproductive gains are subject to Parker's (1990) loaded raffle: if $W_A(X, Y)$ denotes the favoured male's expected reproductive gain from the female and $W_B(X, Y)$ that of the disfavoured male, then

$$W_A(X, Y) = \frac{X}{X + rY} Kg(T), \quad W_B(X, Y) = \frac{rY}{X + rY} Kg(T); \quad (3)$$

or, on using equation (2),

$$W_A(X, Y) = \frac{KX(X + rY)}{(X + rY)(\epsilon + X + rY)}, \quad (4)$$

$$W_B(X, Y) = \frac{KrY(X + rY)}{(X + rY)(\epsilon + X + rY)}.$$

Note that $W_B(X, Y)/W_A(X, Y) = r$: when sperm expenditures are equal, the disfavoured male's gain is lower than that of the favoured male by the loading factor r . Note

Figure 1. Sperm expenditures at the ESS as a function of loading factor r for fixed $\delta = \sqrt{\epsilon\gamma}$, in favoured role A (solid curve), in disfavoured role B (dashed curve), and in either role when $\delta = 0$ (dotted curve). Here ϵ is the number of sperm that would fertilize half of the egg set and γ is the marginal-cost parameter (see equation (11)). Sperm expenditure is measured in units of γ^{-1} along the vertical axis. (Units of ϵ would preclude a comparison with the result for $\epsilon = 0$.)

also that $W_A(X, T) + W_B(X, T) = Kg(T)$: because a female always mates exactly twice, the sum of reproductive gains for her mates must equal her expected future reproductive success.

Following Parker (1990), I assume that there is a trade-off between effort spent on sperm and effort spent on obtaining matings. So the cost of a mating in terms of expected future reproductive success increases with sperm expenditure, ultimately at a prohibitive rate. Accordingly, denoting sperm expenditure by s (which may be either X or T) and mating cost by $Kc(s)$, so that $c(s)$ is a dimensionless quantity, I assume

$$c(0) = 0, \quad c'(s) > 0, \quad c''(s) \geq 0. \quad (5)$$

Thus c is a convex increasing function. Note that $c'(s)$ has dimensions (sperm) $^{-1}$, and so, for fixed c (as in figure 1),

Figure 2. Sperm expenditures at the ESS as a function of $\delta = \sqrt{\epsilon\gamma}$ for fixed ϵ and r . As in figure 1, the solid curve is for favoured role A and the dashed curve for disfavoured role B. Here, however, the dotted curve shows the ratio of expenditure in role B to that in role A. Sperm expenditure is measured in units of ϵ along the vertical axis. (Units of γ^{-1} , as in figure 1, cannot be used because γ varies. Note that $v_1 \rightarrow \infty$, $v_2 \rightarrow \infty$ as $\gamma \rightarrow 0$.)

$$\delta = \sqrt{\epsilon c'(0)}, \quad (6)$$

is a dimensionless measure of uncertainty of fertilization in the absence of competition: the lower the value of δ , the lower the amount of sperm with which an uncontested male can expect to fertilize a given egg set. I assume that the egg set can be fertilized by a relatively small amount of sperm by requiring

$$\delta < 1. \quad (7)$$

Note that Parker (1990) in effect assumed $\delta = 0$. For fixed ϵ (as in figure 2), on the other hand, δ is a dimensionless measure of marginal cost.

Let p_A denote the probability that a mutant focal male is in role A, allocating u_1 against a male who allocates v_2 in role B, so that the focal male's expected reproductive gain from the female is $W_A(u_1, v_2)$. The cost of this mating is $Kc(u_1)$, by assumption, so that the mutant's net increase of expected future reproductive success is $W_A(u_1, v_2) - Kc(u_1)$. Similarly, let $p_B = 1 - p_A$ denote the probability that the mutant is in role B, allocating u_2 against a male who allocates v_1 in role A, so that its net reward is $W_B(v_1, u_2) - Kc(u_2)$. Note that p_A is the proportion of unmated females when mating first is favoured, whereas p_B is the proportion of unmated females when mating second is favoured. On multiplying the reward from each role by the probability of occupying that role and adding, the reward to a u -strategist in a population of v -strategists becomes

$$f(u, v) = p_A \{W_A(u_1, v_2) - Kc(u_1)\} + p_B \{W_B(v_1, u_2) - Kc(u_2)\}. \quad (8)$$

On using equations (3)–(4),

$$f(u, v) = p_A K \left\{ \frac{u_1 g(u_1 + rv_2)}{u_1 + rv_2} - c(u_1) \right\} + p_B K \left\{ \frac{ru_2 g(v_1 + ru_2)}{v_1 + ru_2} - c(u_2) \right\} \quad (9)$$

$$\begin{aligned}
 &= p_A K \left\{ \frac{u_1(u_1 + rv_2)}{(u_1 + rv_2)(\epsilon + u_1 + rv_2)} - c(u_1) \right\} \\
 &+ p_B K \left\{ \frac{ru_2(v_1 + ru_2)}{(v_1 + ru_2)(\epsilon + v_1 + ru_2)} - c(u_2) \right\}. \quad (10)
 \end{aligned}$$

3. THE EVOLUTIONARILY STABLE STRATEGY

Strategy v is a (strong) evolutionarily stable strategy or ESS in the sense of Maynard Smith (1982) if it is uniquely the best reply to itself, i.e. if $f(v, v)$ exceeds $f(u, v)$ whenever $u \neq v$. In Appendix A, I establish that there is a unique ESS, which does not depend on p_A or p_B because each male ‘knows’ which role it is in. The ESS depends, however, on a critical value of the loading factor r , say r_c . If $r > r_c$, then $v_1 > 0, v_2 > 0$ at the ESS; but if $r \leq r_c$, then $v_2 = 0$ at the ESS and v_1 is the optimal amount of sperm to allocate in the absence of any competition. Furthermore, $v_1 = v_2$ at the ESS if and only if either the raffle is fair ($r = 1$) or there is zero risk of failing to fertilize the egg set in the absence of competition, regardless of sperm expenditure ($\epsilon = 0$).

These results hold regardless of whether cost varies nonlinearly or linearly with sperm expenditure. Nevertheless, they are most transparent when cost varies linearly, and so for the sake of clarity I assume henceforth that

$$c(s) = \gamma s, \quad (11)$$

where the constant marginal-cost parameter γ has dimensions (sperm)⁻¹. Then, from Appendix A,

$$r_c = \sqrt{\epsilon\gamma} = \delta \quad (12)$$

(where δ is defined by equation (6)) and sperm expenditures in roles A and B at the ESS are defined by

$$\gamma v_1 = \begin{cases} \delta(1 - \delta) & \text{if } 0 \leq r \leq \delta \\ \frac{\sqrt{r^2 + 4\delta^2 r(1+r)} - 2\delta^2 r(1+r) + r}{2(1+r)^2} & \text{if } \delta < r \leq 1 \end{cases} \quad (13)$$

$$\text{and} \quad \gamma v_2 = \begin{cases} 0 & \text{if } 0 \leq r \leq \delta \\ \frac{2\delta^2(r^2 - \delta^2)}{r\{2\delta^2(1+r) - r^2 + r\sqrt{r^2 + 4\delta^2 r(1+r)}\}} & \text{if } \delta < r \leq 1, \end{cases} \quad (14)$$

respectively. Note that, because γ has dimensions (sperm)⁻¹, the expressions defined by equations (13)–(14) are dimensionless quantities.

Sperm expenditures at the ESS are plotted against r in figure 1 in units of γ^{-1} (i.e., the right-hand sides of equations (13)–(14) are plotted). In each diagram, the solid curve corresponds to favoured role A and the dashed curve to disfavoured role B. The dotted curve corresponds to $\delta = 0$, when sperm expenditure is the same in either role because equations (13)–(14) reduce to $v_1 = v_2 = \sigma$, where

$$\sigma = \frac{r}{\gamma(1+r)^2}. \quad (15)$$

The result that $v_1 = v_2$ when $\delta = 0$ was first obtained by Parker (1990, p.123). Indeed equation (15) reduces to one

of Parker’s equations when $\gamma = 1/2$ (despite his use of a multiplicative model).

The form of the ESS depends on whether δ exceeds 0.5. If not, i.e. if $0 < \delta \leq 1/2$, then the maximum possible expenditure at the ESS is always $0.25/\gamma$, precisely the same value as when fertilization is assured ($\delta = 0$), but the maximum occurs where $r = 1/(1 + 4\delta^2)$ instead of at $r = 1$ (as in Parker’s model). If $1/2 < \delta < 1$, on the other hand, expenditure is always lower than when fertilization is assured, the maximum occurring where $r \leq \delta$, i.e. in the absence of competition. In both cases, however, $v_1 - v_2$ is a strictly decreasing function of r when $\delta < r \leq 1$. In other words, the divergence between expenditures in roles A and B increases with unfairness in the *de facto* competitive domain.

Figure 2 shows the same ESS as a function of $\delta = \sqrt{\epsilon\gamma}$ for fixed ϵ and r . Thus, in effect, it shows how sperm expenditure varies with marginal cost: the lower the value of γ , the higher the values of both v_2 (dashed) and v_1 (solid), and the higher the value of their ratio (dotted). From this perspective, the critical loading factor below which $v_2 = 0$ is replaced by a critical marginal cost above which $v_2 = 0$. I discuss this point further in § 4.

4. DISCUSSION

Using an idealized model to elucidate the effect of sperm limitation on sperm competition, I have shown in this paper that the slightest risk of incomplete fertilization in the absence of sperm competition is enough to ensure that favoured males expend more than disfavoured males in the presence of sperm competition, unless the competition is perfectly fair. The ESS depends on both the degree of uncertainty, as measured by the parameter ϵ defined in § 2, and the unfairness of the competition, as measured by the loading factor r . The competition is fair only if $r = 1$, and unfairness increases as r decreases. Only if $\epsilon = 0$ or $r = 1$ are expenditures equal. Otherwise, regardless of the probability of occupying either role, (i) expenditure is greater in the favoured role than in the disfavoured role, and (ii) the divergence increases with unfairness. The first of these results contradicts a qualitative conclusion from Parker’s (1990) multiplicative model, for the reasons stated in § 1.

The ESS also depends on the marginal cost of mating with respect to sperm expenditure, as measured by the parameter γ introduced in § 3. Note that γ is not the energetic cost of producing a unit of sperm, but rather the opportunity cost in (foregone) expected future reproductive success of releasing an additional unit of sperm. Thus γ is extremely difficult to measure, but its value does not affect the model’s qualitative predictions. In particular, because opportunity cost increases with mating frequency, the model predicts lower expenditures in either role when mating frequency is higher, as well as zero expenditure in the disfavoured role above a critical mating frequency (see figure 2). Now, in principle, γ is the same for every male in my model population. In practice, however, one would expect a more elaborate model where γ varies among individuals to yield an ESS at which sperm expenditure is higher for males with lower opportunity costs, and hence for males with lower mating frequencies. This ESS would reflect the observation by

Warner *et al.* (1995) that *T. bifasciatum* males with very low mating success release very high numbers of sperm.

Incomplete fertilization risk is not, however, the only effect that produces greater sperm expenditure in the favoured role than in the disfavoured role at the ESS. As remarked already in §1, if the fairness of the fertilization raffle to a disfavoured second male is not constant, as Parker (1990) assumed, but decreases with the amount of sperm expended by the favoured first male, then once again expenditure is greater in the favoured role than in the disfavoured role (Mesterton-Gibbons 1999). Thus virtual equality of sperm expenditure in nature (despite the existence of a favoured role) suggests not only that roles are randomly assigned (with arbitrary probabilities), but also both that fairness is virtually constant and that there is virtually no risk that an ejaculate will fail to fertilize a set of eggs in the absence of sperm competition.

This result may be important biologically because relatively little is known at present about the mechanisms underlying sperm competition. For example, Birkhead & Parker (1997, pp. 139–140) use indirect evidence (potential correlates of sperm transfer) that sperm expenditures are virtually equal between ‘queueing’ pairs of *S. tridecemlineatus* males to infer only that the evidence appears consistent with roles being randomly assigned. My game-theoretic analysis suggests, however, that the evidence appears consistent only if fairness is independent of sperm expenditure and there is virtually no risk of failing to fertilize an egg set in the absence of sperm competition. In other words, my analysis suggests that apparent equality of sperm expenditures in nature may be evidence not only of roles being randomly assigned, but also of several other characteristics of the underlying mechanisms about which so little is known.

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APPENDIX A. ESS CALCULATION

The purpose of this appendix is to calculate the ESS of the game whose reward function is defined by equations (9)–(10). Because g is increasing and bounded above whereas c is increasing and unbounded, the function f defined by equation (9) must have a maximum with respect to u_1 where $u_1 = 0$ or $u_1 > 0$ according to whether $\partial f / \partial u_1|_{u_1=0}$ is non-positive or positive, and with respect to u_2 where $u_2 = 0$ or $u_2 > 0$ according to whether $\partial f / \partial u_2|_{u_2=0}$ is non-positive or positive. Partial differentiation reveals that

$$\frac{\partial f}{\partial u_1} = p_A K \left\{ \frac{rv_2 g(u_1 + rv_2) + u_1(u_1 + rv_2)g'(u_1 + rv_2)}{\{u_1 + rv_2\}^2} - c'(u_1) \right\}, \quad (A1)$$

and

$$\frac{\partial f}{\partial u_2} = p_B K \left\{ \frac{rv_1 g(v_1 + ru_2) + r^2 u_2(v_1 + ru_2)g'(v_1 + ru_2)}{\{v_1 + ru_2\}^2} - c'(u_2) \right\}, \quad (A2)$$

where a prime denotes differentiation with respect to argument. Thus f is maximized with respect to u_1 where

$$\begin{aligned} u_1 &= 0 \text{ if } rc'(0)v_2 \geq g(rv_2), v_2 > 0 \text{ or } c'(0) \geq g'(0), v_2 = 0 \\ \partial f / \partial u_1 &= 0 \text{ if } rc'(0)v_2 < g(rv_2), v_2 > 0 \text{ or } c'(0) < g'(0), v_2 = 0, \end{aligned} \quad (A3)$$

and with respect to u_2 where

$$\begin{aligned} u_2 &= 0 \text{ if } c'(0)v_1 \geq rg(v_1), v_1 > 0 \text{ or } c'(0) \geq rg'(0), v_1 = 0 \\ \partial f / \partial u_2 &= 0 \text{ if } c'(0)v_1 < rg(v_1), v_1 > 0 \text{ or } c'(0) < rg'(0), v_1 = 0. \end{aligned} \quad (A4)$$

Together, these equations yield the unique best-reply strategy $u = (u_1, u_2)$ to every possible population strategy v . If v is the unique best reply to itself, however, then v is also the unique strong ESS. Thus $v = (v_1, v_2)$ is the unique strong ESS if equation (A3) is satisfied with $u_1 = v_1$ and equation (A4) is satisfied with $u_2 = v_2$. Note that these results are valid for the most general form of g considered in §2 and for any c that satisfies (5).

Henceforward, however, I assume that g is defined by equation (2), hence f by equation (10). It is then impossible to satisfy equations (A3)–(A4) with $u_1 = v_1 = 0$ and $u_2 = v_2$. For suppose that these equations hold. Then, because now $g'(0) = 1/\epsilon$, equations (6) and (7) imply $g'(0) > c'(0)$, so that equation (A3) implies $rc'(0)v_2 \geq g(rv_2), v_2 > 0$ and, as a consequence, equation (A4) implies $c'(0) < rg'(0)$. Thus, from equation (2), $c'(0)\{\epsilon + rv_2\} \geq 1$ and $r > \epsilon c'(0)$ must be satisfied simultaneously. Furthermore, $v_2 > 0$ requires $\partial f / \partial u_2|_{u_2=v_2} = 0$, which reduces to $\{\epsilon + rv_2\}^2 c'(v_2) = r\epsilon$. Hence $rc'(0)^2 \geq c'(v_2)$, which is compatible with $\epsilon c'(0) < r \leq 1$ only if $c'(0) > c'(v_2)$, contradicting equation (5). Therefore, at the ESS, $\partial f / \partial u_1|_{u_1=v_1} = 0$, or

$$rv_2(\epsilon + v_1 + rv_2) + \epsilon v_1 = (\epsilon + v_1 + rv_2)^2 (v_1 + rv_2) c'(v_1). \quad (A5)$$

On the other hand, given $u_1 = v_1 > 0$, equation (A4) can be satisfied either with $u_2 = v_2 = 0$ or with $u_2 = v_2 > 0$. In the first case, equation (A4) implies $c'(0)v_1 \geq rg(v_1)$ or, on using equation (2), $r \leq (\epsilon + v_1)c'(0)$, where $(\epsilon + v_1)^2 c'(v_1) = \epsilon$, by equation (A5). Thus there exists a critical loading factor, below which the disfavoured male deposits no sperm at the ESS while the favoured male deposits the amount of sperm that would be optimal in the absence of competition. In the second case, $\partial f / \partial u_2|_{u_2=v_2} = 0$, or

$$rv_1(\epsilon + v_1 + rv_2) + r^2 \epsilon v_2 = (\epsilon + v_1 + rv_2)^2 (v_1 + rv_2) c'(v_2). \quad (A6)$$

Together, equations (A5) and (A6) now imply that $v_1 = v_2$ is possible only if $r = 1$ (the raffle is fair) or $\epsilon = 0$ (zero risk of failing to fertilize the egg set in the absence of competition, regardless of sperm expenditure).

In the case where marginal costs are constant, i.e. where $c'(v_1) = c'(v_2) = \gamma$, equations (A5) and (A6) reduce to

$$\begin{aligned} r\gamma v_2(\delta^2 + \gamma v_1 + r\gamma v_2) + \delta^2 \gamma v_1 &= (\delta^2 + \gamma v_1 + r\gamma v_2)^2 (\gamma v_1 + r\gamma v_2) \\ &= r\gamma v_1(\delta^2 + \gamma v_1 + r\gamma v_2) + r^2 \delta^2 \gamma v_2. \end{aligned} \quad (A7)$$

Routine calculations now readily establish that equations (13)–(14) yield the only positive solution pair.

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