Sperm competition games: a prospective analysis of risk assessment

G. A. PARKER¹, M. A. BALL², P. STOCKLEY¹ AND M. J. G. GAGE¹

¹*Population Biology Research Group, School of Biological Sciences, University of Liverpool, Liverpool L69 3BX, UK*
(gap@liverpool.ac.uk)

²*Department of Mathematical Sciences, University of Liverpool, Liverpool L69 3BX, UK*

SUMMARY

We develop the logic of assessment of sperm competition risk by individual males where the mechanism of sperm competition follows a 'loaded raffle' (first and second inseminates of a female have unequal prospects). Male roles (first or second to mate) are determined randomly. In model 1, males have no information about the risk associated with individual females and ejaculation strategy depends only on the probability, q , that females mate twice. Evolutionarily stable strategy (ESS) ejaculate expenditure increases linearly from zero with q , and reduces with increasing inequality between ejaculates, though the direction of the loading (which role is favoured) is unimportant. In model 2, males have perfect information and can identify each of three risk states: females that will (1) mate just once ('no risk'), (2) mate twice but have not yet mated ('future risk'), and (3) mate twice and have already mated ('past risk'). The ESS is to ejaculate minimally with 'no risk' females, and to expend equally with 'past' and 'future' risk females; the direction of the competitive loading is again unimportant. Expenditure again increases with risk, but is now non-zero at extremely low risk. Model 3 examines three cases of partial information where males can identify only one of the three risk states and cannot distinguish between the other two: they therefore have just two information sets or 'contexts'. Expenditure in both contexts typically rises non-linearly from zero with q , but (whatever the loading direction) expenditure is higher in the context with higher risk (e.g. if contexts are 'mated' and 'virgin', males spend more with mated females). However, in highly loaded raffles, sperm expenditure can decrease over part of the range of risk. Also, the direction of the loading now affects expenditure. Biological evidence for the predictions of the models is summarized and discussed.

1. INTRODUCTION

The predicted response to sperm competition within a species can be very different from that predicted across species. Across species, average ejaculate expenditure is expected universally to increase with sperm competition level (see Parker 1998). Within species, the reverse may apply. A simple model of group spawning in which males can assess the number of competitors predicted that as the number of males increases above two, ejaculate expenditure per male gradually reduces (Parker *et al.* 1996). This conclusion was upheld in a more complex analysis allowing continuous fertilization and strategic variation in sperm size, except that ejaculate effort could decline as the number of males increases above one (Ball & Parker 1997).

The present paper concerns assessment of sperm competition risk when sperm competition is much less intense. It relates to a species where typically for a proportion $1-q$ of females, mating occurs only once before fertilization of their eggs, and for a proportion q , mating occurs twice so that the two ejaculates compete. Parameter q is seen as a range of sperm

competition 'risk' to distinguish it from a range of 'intensity', where several ejaculates compete for each set of eggs (Parker *et al.* 1996). Previous 'risk' models predicted increased ejaculate expenditure with increased risk, viewed both across (Parker 1982) and within species (Parker 1990*b*). Note that there is no conflict with the above 'intensity' model prediction (Parker *et al.* 1996). In 'risk' models, we are solely concerned with the range between 'no sperm competition' and 'sperm competition' between just two ejaculates. In 'intensity models' we investigate numbers of two and above ejaculates. There is growing evidence that males may change their ejaculate dose in response to local conditions relating to the risk of sperm competition (§6). The analysis relates mainly to internally fertilizing species, but also applies to external fertilizers in which either one or two ejaculates are typically involved in fertilization.

We here further develop the logic of assessment of sperm competition risk by males, by developing models of male ability to discriminate between female mating states. Biological evidence supports some of the predictions. In our first model, males have no information so

that their ejaculation strategy is the same with all females, tuned only by the average risk, q , of double-mating. This is compared with the case of perfect information, where a male can identify, on encountering a female, what the mating pattern of that female is likely to be. We then examine three cases of imperfect information in which males can identify only one of three possible situations: (i) females that mate just once, (ii) females that have already mated, (iii) females that will mate again in the future. A companion paper (Ball & Parker 1998b) analyses cases where males make mistakes: a male meeting a female in one situation has a finite probability of identifying her as belonging to either of the other two situations.

Since the models developed here analyse how males should allocate sperm, for simplicity we do not include possible female strategies of sperm selection, despite their current interest (e.g. Zeh & Zeh 1996a,b). Provided that female interests do not relate directly to male sperm allocation strategies, we do not anticipate qualitatively different conclusions by omitting female strategies.

2. ANALYSIS

(a) Definitions of sperm competition risk

One of us (G.A.P.) recently discovered an unfortunate confusion in definitions involving 'risk' models in sperm competition games, stemming from the first approach (Parker 1982) and continuing into recent analyses (Parker 1984b, 1990b, 1993; Parker & Begon 1993; Ball & Parker 1996; Birkhead & Parker 1997). All these prior analyses relate to risk defined strictly as the probability, p , that a given male, when mating, will face sperm competition from one other ejaculate. This is not equivalent to q , the probability of occurrence of sperm competition in the population (i.e. the females' probability of double-mating). During the prior analyses, p came to be regarded (incorrectly) as synonymous with q , when in fact all calculations actually related to p .

The relation between the two definitions is easily defined for an internally fertilizing species (the terminology can readily be altered to cover external fertilization). If q is the probability that females mate twice, in a population containing F receptive females there are $F[(1-q) + 2q] = F(1+q)$ matings per mating period, of which $F(1-q)$ are with females that mate once, and $2Fq$ are with females that mate twice (every double-mating involves two copulations). Of a total of $F(1+q)$ matings, males face sperm competition on $2Fq$ occasions, so the probability that a male faces sperm competition at a given copulation is $p = 2q/(1+q)$, and the probability that he will not is $1-p = (1-q)/(1+q)$.

Following previous approaches, we assume that q is determined extrinsically, i.e. it is not a function of male sperm allocation strategy (but, see Shapiro & Giraldeau 1996).

Note also that if q is independent of the number of males and females, then p is also independent of sex ratio. We can readily envisage situations in which there are such dependencies (Ball & Parker 1998a),

but for simplicity these are not examined in the present analysis. ESS solutions in terms of p and q differ only in quantitative detail and not in qualitative predictions (p increases monotonically with q ; $p = q$ at limits 0 and 1, and $p < q$ between the limits). Biologically, solutions are often most useful in terms of q . These versions are given here; they can readily be converted to solutions in p by substituting $q = p/(2-p)$.

(b) Risk states, and knowledge contexts

A male about to mate with a female with a given set of eggs may encounter three different sperm competition risk states (a more advanced analysis may allow more states):

0—the female is a virgin that will mate now but not again;

1—the female is a virgin that will mate now and again once;

2—the female has mated once and will mate now but not again.

The word 'virgin' is defined in this context in relation to a mating period, i.e. to the set of eggs competed for. These states may either be an intrinsic property of the female, or a property of her circumstances (e.g. another male is present or absent). A male's strategy specifies the number of sperm he ejaculates when he assesses a female to be in a given state, or set of states, e.g.

s_0 —on assessing the female to be in state 0;

s_1 —on assessing the female to be in state 1;

$s_{0,1}$ —on assessing the female to be in either state 0 or 1; etc.

What a male should do depends on his ability to discriminate between the states. The present paper concerns special cases where males can recognize certain states, or sets of states, but cannot discriminate between others. What a male can identify is termed a *context* ('the conditions and circumstances that are relevant to an event'); it is equivalent to an information set. His strategy is a definition of what he does in a given context. If, say, a male cannot discriminate between females in states 0, and 1, but can identify state 2 females, we would seek two strategies, $s_{0,1}$ and s_2 , corresponding to the two contexts, (0,1) and (2). If males cannot discriminate at all, there is only one context (0,1,2), and we therefore investigate the single strategy $s_{0,1,2}$. In a companion paper (Ball & Parker 1998b), we examine the problem of misidentifications of states (mistakes).

(c) General analysis

Techniques for analysis of sperm competition games have been given elsewhere (e.g. Parker 1993); the following serves as a general outline. Males can vary sperm numbers, s_i , continuously in context i . Let s_i^* be the evolutionarily stable strategy (ESS, Maynard Smith 1982) for sperm numbers in context i , and let strategy I be the ESS across all contexts (I is $s_i^*, s_j^*, \dots, s_n^*$). Denoting $W(s_i, I)$ as the fitness of a rare mutant deviating by playing $s_i \neq s_i^*$ in a population playing I , we find the ESS by setting

$$\left[\frac{\delta W(s_i, I)}{\delta s_i} \right]_{s_i=s_i^*} = 0; \quad (1a)$$

subject to

$$\left[\frac{\delta^2 W(s_i, I)}{\delta s_i^2} \right]_{s_i=s_i^*} < 0, \quad (1b)$$

to ensure that s_i^* is a maximum (e.g. see Maynard Smith 1982).

We assume that expenditure on gaining matings determines the number of matings a male achieves, and that his ejaculate expenditure determines the expected value of each mating. There is a trade-off so that increasing ejaculate expenditure increases gain per mating, but reduces the number of matings (some evidence exists for such a trade-off; see Warner *et al.* 1995).

A mutant male's fitness is his number of matings achieved, $n(s_i, I)$, times the expected value of each mating, $v(s_i, I)$:

$$W(s_i, I) = n(s_i, I) \times v(s_i, I) \quad (2)$$

and from equation (1a) this occurs when (Parker 1993):

$$-\left[\frac{n(s_i, I)}{n'(s_i, I)} \right]_{s_i=s_i^*} = \left[\frac{v(s_i, I)}{v'(s_i, I)} \right]_{s_i=s_i^*}; \quad (3)$$

where primes denote the differential coefficients of n or v with respect to s_i . Note that n' is negative.

(d) Functions $n(s_i, I)$ and $v(s_i, I)$

The exact forms of n and v depend on the model, and are dealt with separately. The general logic is as follows. Consider first n —the number of matings achieved. Each male has a fixed total energy budget of R units, and the average cost of obtaining each mating (finding a female, etc.) is C units. The cost of each unit mass of ejaculate is D , so the cost of an ejaculate containing s_i units of sperm is Ds_i . R , C , and D are all expressed in the same energy units. Let S_i be the average sperm number per mating, averaged across all mating contexts, played by a mutant deviating only in context i , and let S^* be the same average for an I -player. Thus, where $p_i, p_j, \dots$ etc. are the probabilities that a male mates in contexts $i, j, \dots$ etc., $S_i = (p_i s_i + p_j s_j^* + \dots \text{etc.})$, and $S^* = (p_i s_i^* + p_j s_j^* + \dots \text{etc.})$.

The number of matings gained by the mutant male is

$$n(s_i, I) = \left(\frac{R}{C + D\langle S_i \rangle} \right). \quad (4)$$

In previous analyses, this quantity was expressed relative to the ESS number of matings per male [$R/(C + D\langle S^* \rangle)$], but such a scaling is redundant since it cancels out in equation (3), giving the same result as the unscaled version (4).

The function $v(s_i, I)$, the average value of each mating for a mutant playing ejaculate expenditure s_i against an I population, depends on the probability and mechanism of sperm competition. We assume that the mechanism of sperm competition follows a 'loaded raffle' (Parker 1990a). When a female contains

ejaculates from two males, sperm from the second is competitively weighted by a factor r , relative to sperm from the first. Thus, the proportionate gains to each male are: $(s_1/(s_1 + rs_2))$ for male 1; and $(rs_2/(s_1 + rs_2))$ for male 2.

(e) ESS ejaculate expenditures

The quantity we seek is the dimensionless value E_i^* , the ESS expenditure on the ejaculate by a male mating in context i , expressed as a proportion of the total cost of a mating (cost of acquiring a female and then mating), averaged across all contexts:

$$E_i^* = \left(\frac{Ds_i^*}{C + D\langle S^* \rangle} \right). \quad (5)$$

This yields solutions that are independent of constants C and D (see below). Expressions in terms of absolute sperm expenditure (Ds_i^*) are required if, say, the biological effects of C are to be investigated.

3. MODEL 1: MALES HAVE NO INFORMATION ABOUT RISK

Here, a male has no information about the risk of sperm competition when he meets females. His strategy is shaped by the species-level risk of sperm competition between two ejaculates, q . We assume that when sperm competition occurs, a given male is equally likely to mate first or second (i.e. roles are random *sensu* Parker (1990a)), but that he has no information about roles. Thus, there is only one context and one strategy, $s_{0,1,2}$, since the male must treat all matings equally. The average sperm number of the mutant is $S_{0,1,2} = s_{0,1,2}$, and the average for an ESS player is $S^* = s_{0,1,2}^*$. Thus,

$$-\left[\frac{n(s_{0,1,2}, I)}{n'(s_{0,1,2}, I)} \right]_{s_{0,1,2}=s_{0,1,2}^*} = \left(\frac{C + D\langle S^* \rangle}{D} \right). \quad (6)$$

The average value of a mating for an $s_{0,1,2}$ -player in a population playing I is

$$v(s_{0,1,2}, I) = \left\{ (1-q) \frac{s_{0,1,2}}{s_{0,1,2}} + q \left(\frac{s_{0,1,2}}{s_{0,1,2} + rs_{0,1,2}^*} \right) + q \left(\frac{rs_{0,1,2}}{rs_{0,1,2} + s_{0,1,2}^*} \right) \right\} / (1+q). \quad (7)$$

Note that gains with the $(1-q)$ females that copulate only once are independent of $s_{0,1,2}$, which cancels out since there is no sperm competition. For each such mating, a male encounters q females who will mate again in the future and q females who have already mated. We obtain

$$\left[\frac{v(s_{0,1,2}, I)}{v'(s_{0,1,2}, I)} \right]_{s_{0,1,2}=s_{0,1,2}^*} = \frac{s_{0,1,2}^* (1+r)^2}{2qr}, \quad (8)$$

and from expression (3), equating (6) and (8) gives the ESS proportion of reproductive expenditure spent on the ejaculate (5) as

$$E_{0,1,2}^* = \frac{2qr}{(1+r)^2}. \quad (9)$$

For the case of a fair raffle, $r=1.0$, and each sperm is competitively equal whether transferred in the first or second ejaculate. Thus,

$$E_{0,1,2}^* = \frac{q}{2}, \quad (10)$$

which is analogous to the result of Parker (1984, 1993), that $E_{0,1,2}^* = p/(4-2p)$, and similar to the original solution $E_{0,1,2}^* = p/(4-p)$ obtained by Parker (1982) using a different version of n .

Equation (10) predicts that across the species in which sperm competition approximates to a fair raffle, relative ejaculate expenditure should increase from 0 to 0.5 as the probability of double-mating increases from 0 to 1.0 (figure 1). The solution in terms of p is equal to those in terms of q at 0 and 1, but curve $E_{0,1,2}^*(p)$ is bowed below that of line $E_{0,1,2}^*(q)$.

The effect of competitive loading r , has not previously been investigated. In (9), we see that

$$\frac{r}{(1+r)^2} = \frac{r^{-1}}{(1+r^{-1})^2};$$

and that both are maximized at $r=1.0$ (i.e. under the conditions of a fair raffle). Hence, whether sperm in role 2 have e.g. twice the competitive weight of role 1—or *vice versa*—makes no difference to the ESS, which is therefore unaffected by the ‘loading direction’. The more loaded the raffle, the less the ESS ejaculate expenditure at any given risk, q (see figure 1). Hence, we predict a greater deviation below the line for $r=1.0$ in a species where there is a high degree of loading in favour of one or other ejaculate (high first male advantage, or high second male advantage).

4. MODEL 2: MALES HAVE PERFECT INFORMATION ABOUT RISK AND ROLE

Here a male has perfect information. On encountering a female, he can identify whether a female has already mated, and if not, whether she will mate again in the future. He also therefore ‘knows’ his role (1=first to mate, 2=second to mate), for cases when there will be sperm competition. Roles are again allocated randomly. On meeting a female that will not remate (probability $(1-q)/(1+q)$), we assume that a male transfers an arbitrary minimum amount of sperm. Calling s_1 and s_2 the sperm strategies played in roles 1 and 2 (each occurring with probability $q/(1+q)$), the average number of sperm expended per mating by a mutant male playing $s_1 \neq s_1^*$ in role 1, is $\langle S_1 \rangle = q(s_1 + s_2^*)/(1+q)$, and by a mutant playing $s_2 \neq s_2^*$ in role 2, is $\langle S_2 \rangle = q(s_2 + s_1^*)/(1+q)$. We find that

$$-\left[\frac{n(s_1, I)}{n'(s_1, I)} \right]_{s_1=s_1^*} = -\left[\frac{n(s_2, I)}{n'(s_2, I)} \right]_{s_2=s_2^*} = \left(\frac{C + D\langle S^* \rangle}{D(q/(1+q))} \right),$$

where $\langle S^* \rangle = q(s_1^* + s_2^*)/(1+q)$.

Remembering that a mutant playing $s_1 \neq s_1^*$ in role 1, plays s_2^* in role 2 against an ESS player playing s_1^* , the average relative value of a mating for such a mutant is

Figure 1. Relation between ESS ejaculate expenditure (expressed as a proportion of total expenditure per mating), $E_{0,1,2}^*$, and the frequency of double mating in the population (risk q) when males have no information about female states, and hence ejaculate in only one context (0,1,2). The three lines are for three degrees of loading in the fertilization raffle: $r=1.0$ (bold line, fair raffle), 0.5 (each of male 2's sperm count only half those of male 1), and 0.1 (each of male 2's sperm count only one tenth those of male 1).

$$v(s_1, I) = \left\{ (1-q) + q \left(\frac{s_1}{s_1 + rs_2^*} \right) + q \left(\frac{rs_2^*}{rs_2^* + s_1^*} \right) \right\} / (1+q),$$

so that

$$\left[\frac{v(s_1, I)}{v'(s_1, I)} \right]_{s_1=s_1^*} = \left(\frac{(s_1^* + rs_2^*)^2}{qrs_2^*} \right). \quad (11a)$$

For a mutant playing $s_2 \neq s_2^*$,

$$v(s_2, I) = \left\{ (1+q) - q \left(\frac{s_1^*}{s_1^* + rs_2^*} \right) + q \left(\frac{rs_2}{rs_2 + s_1^*} \right) \right\} / (1+q),$$

Therefore

$$\left[\frac{v(s_2, I)}{v'(s_2, I)} \right]_{s_2=s_2^*} = \left(\frac{(s_1^* + rs_2^*)^2}{qrs_1^*} \right). \quad (11b)$$

Therefore

$$\left(\frac{C + D\langle S^* \rangle}{D(q/(1+q))} \right) = \left[\frac{v(s_1, I)}{v'(s_1, I)} \right]_{s_1=s_1^*} = \left[\frac{v(s_2, I)}{v'(s_2, I)} \right]_{s_2=s_2^*}, \quad (12)$$

and so combining (12) with (11a) and (11b) shows that at the ESS a male must play the same ejaculation strategies in both roles, i.e. $s_1^* = s_2^*$. It is then easy to show that the ESS ejaculate expenditure with double-mating females is

$$E_1^* = E_2^* = \frac{(1+q)r}{(1+r)^2}. \quad (13)$$

Unlike model 1 (figure 1), (13) has a positive value even when $q=0$ (figure 2). Even when female states 1 and 2 are extremely rare, males can identify them. A male meeting a female in state 1 ‘knows’ that she will mate again in the future, and that a state 2 female has

Figure 2. Relation between ESS ejaculate expenditures, $E_1^* = E_2^*$, and the frequency of double mating in the population (risk q) when males have perfect information about female states, and hence ejaculate in three contexts (0), (1), (2). The three lines are for the three degrees of loading in the fertilization raffle as in figure 1. The ESS for state 0 females (where there will be no sperm competition), is some arbitrary minimum expenditure $E_1^* \rightarrow 0$.

mated in the past. Hence, despite their rarity, he must escalate ejaculate expenditure, in contrast to model 1, where states 1 and 2 cannot be identified, so that if their frequency approaches zero, a male should expend close to zero.

Note that (13) contains the same terms for r as (9). So again the 'loading direction' (whether mating first or second is more favourable) does not influence the ESS expenditure—what matters is only the competitive difference. Though the relative effect of 'role' is the same, the strength of the relationship between E^* and q (cf. figures 1 and 2) is less, because (13) has a positive intercept.

For the special case of the fair raffle ($r=1.0$),

$$E_1^* = E_2^* = \frac{(1+q)}{4}, \quad (14)$$

see figure 2.

Since there are $(1-q)/(1+q)$ matings with zero expenditure for every $2q/(1+q)$ matings, expending $E_1^* = E_2^*$, the average ejaculate expenditure is

$$E^* = \frac{0 + 2qE_1^*}{(1+q)} = \frac{2qr}{(1+r)^2},$$

i.e. the same as in the case of no information (equation (9)).

5. MODEL 3: THREE SPECIAL CASES OF PARTIAL INFORMATION

We now examine the three possible cases where males can recognize only one out of the three female states. In the first, males can identify only 'past risk' (state 2 females, which contain sperm from a past mating), but cannot distinguish between 'future risk' and 'no risk' females (states 0 and 1). In the second, males can identify only 'future risk' (state 1), and in the third, males can identify only 'no risk' (state 0) females.

(a) Recognition of past risk

There are two contexts, 2 and (0,1), since males recognize mated females, but cannot discriminate between virgins that will mate only once and those that will mate twice. We therefore seek s_2^* and $s_{0,1}$. Average sperm numbers per mating are $\langle S_{0,1} \rangle = (s_{0,1} + qs_2^*)/(1+q)$ for a mutant playing $s_{0,1} \neq s_{0,1}^*$, and $\langle S_2 \rangle = (s_{0,1}^* + qs_2)/(1+q)$ for a mutant playing $s_2 \neq s_2^*$. Thus,

$$-\left[\frac{n(s_{0,1}, I)}{n'(s_{0,1}, I)} \right]_{s_{0,1}=s_{0,1}^*} = \left(\frac{C + D\langle S^* \rangle}{D/(1+q)} \right), \quad (15a)$$

$$-\left[\frac{n(s_2, I)}{n'(s_2, I)} \right]_{s_2=s_2^*} = \left(\frac{C + D\langle S^* \rangle}{qD/(1+q)} \right) \quad (15b)$$

where $\langle S^* \rangle = (s_{0,1}^* + qs_2^*)/(1+q)$.

The average value of a mating for the two mutants is given by a pair of equations parallel to those of the previous section, and we thus obtain equations parallel to (11a) and (11b) with $s_{0,1}$ substituted for s_1 . By the same technique, we are then able to show that

$$s_{0,1}^* = qs_2^*, \quad (16)$$

and hence, $s_{0,1}^* < s_2^*$, as would be expected. Note that the ratio of sperm numbers in the two contexts is independent of loading factor r . From (15a), (15b), (16) and the analogues of (11a), (11b),

$$E_{0,1}^* = \frac{q^2(1+q)r}{(q+r)^2}; \quad (17a)$$

$$E_2^* = \frac{q(1+q)r}{(q+r)^2}; \quad (17b)$$

and so for a fair raffle,

$$E_{0,1}^* = \frac{q^2}{(1+q)}; \quad (18a)$$

$$E_2^* = \frac{q}{(1+q)}. \quad (18b)$$

Solutions for $E_{0,1}^*$ and E_2^* are plotted against q in figure 3. As evident from (17a) and (17b), whatever the magnitude or direction of the competitive loading (i.e. whether the first or the second mating is favoured), $E_2^* > E_{0,1}^*$, so that curves for E_2^* (figure 3b) are above those for $E_{0,1}^*$ (figure 3a), at all intermediate values for q . Under the fair raffle, the greatest difference ($E_2^* - E_{0,1}^*$) can be calculated to occur at $q=0.38$. However, the effect of competitive loading is now more complex: it now exerts an effect because of the asymmetry in information about the risk between contexts. ESS expenditure is always greater when the male mating second is disfavoured (compare pairs of curves in figure 3a or b). This is particularly noticeable in figure 3b: under high competitive disadvantage to the second male, E_2^* rises to a peak at relatively low q (around $q=0.1$ for $r=0.1$ curve; figure 3b), and then declines as q increases. Thus, in highly loaded raffles, sperm expenditure can decrease with risk over part of the range.

Figure 3. Relation between ESS ejaculate expenditures and the frequency of double-mating in the population (risk q) when males can distinguish only between virgin and mated females, hence they ejaculate in two contexts (0,1), and (2). (a) shows the ESS expenditure with virgins, i.e. females in states (0, 1), and (b) shows the ESS expenditure with mated females, i.e. in state (2). The bold line is for a fair raffle ($r=1.0$), and the pairs of dotted lines are for the alternative 'directions' of a given competitive loading (see text). The ESS for the case where males can identify only state 1 females, hence they ejaculate in two contexts (1), and (0,2) is the same, but the r values are reversed in each pair of curves.

Why do E^*_2 and $E^*_{0,1}$ converge at the limits of q ? As q approaches zero, virtually no females mate twice. Since the risk of future mating is so tiny, a male mating with a virgin expends only a minute amount of sperm. Thus, a male identifying a mated female has only an infinitesimal amount of sperm to compete against (see also Ball & Parker 1998b). At $q=1$, all females mate twice, so there is no asymmetry of information between contexts (mated and unmated). Then $E^*_2 = E^*_{0,1}$ at all r , and only the ratio (not the direction) of loading is important.

In figure 3, differences between E^*_2 and $E^*_{0,1}$ at given q and r show the variation expected due to intraspecific assessments. Changes across q and r indicate the variation expected across species in relation to their sperm competition risk (q) or mechanism of sperm competition (r). The fact that difference between E^*_2 and $E^*_{0,1}$ is greatest at some intermediate value of q has important implications for comparative studies, as are the distortions due to r .

Figure 4. Relation between the average ESS ejaculate expenditures (across both contexts) and the frequency of double-mating in the population (risk q) for the case examined in figure 3, when males can distinguish only between virgin and mated females. The bold line is for a fair raffle ($r=1.0$), and the pairs of dotted lines are for the alternative 'directions' of a given competitive loading (see text). The ESS for the case where males can identify only state 1 females, hence they ejaculate in two contexts (1), (0,2) is the same, but the r values are reversed in each pair of curves.

From equations (17a) and (17b) the average relative ejaculate expenditure is

$$E^* = \frac{E^*_{0,1} + qE^*_2}{(1+q)} = \frac{2q^2r}{(q+r)^2}, \quad (19)$$

which always increases with risk (figure 4), though not linearly as in figure 1. With a high competitive loading favouring first matings (e.g. curve for $r=0.1$), the relation between E^* and q may be weak across all but the lowest range of q .

(b) Recognition of future risk

Males can identify future risk, but have no information about past risk. They play s_1 on identifying a future risk female, and $s_{0,2}$ on identifying a female that will not mate again in future (it may, or may not, have already mated). We find expressions relating to $s^*_{0,2}$ and s^*_1 in the same way as before, showing that

$$s^*_{0,1} = q s^*_1, \quad (20)$$

(cf. equation (16)), and then solve for $E^*_{0,2}$ and E^*_1 . The result is intuitively satisfying: ESS results are equivalent to the previous case but with the loading direction reversed.

The same conclusion about inverse loadings applies to the average expenditures, E^* , for these two special cases. The ESS is equal to equation (19) with r inverted: a strong first male advantage in the 'past risks' model gives the same effect as an equally strong second male advantage in the 'future risks' model. A regression of phylogenetic contrasts for relative testis size (assuming this is equivalent to E^*) against sperm competition risk may help to reveal recognition biases across species where sperm competition outcomes are known. Where males can recognize only past risk,

such regressions are likely to be characterized at low q by showing species with a strong first male advantage clustered above the regression line, and those with a strong second male advantage below it. The opposite would be true for species where males can recognize only future risk.

For the case of a fair raffle, there are no competitive asymmetries between ejaculates ($r=1.0$). The average expenditure is then equal for the two cases (recognition of future risk, past risk):

$$E^* = \frac{2q^2}{(1+q)^2} \quad (21)$$

(c) Recognition of zero risk

If males can identify females that will mate only once ('no risk', state 0 females), but cannot discriminate between the two risk states (state 1, 2 females), we obtain exactly the same solutions as already obtained in model 1 for perfect information. If roles are random, the ESS ejaculate expenditure is the same in both risk states (1 and 2)—it does not matter whether a female has already mated or will do so in the future (see equation (13)). Thus the ESS is for males to spend an arbitrary minimum when they identify a female that will mate only once ($E_0^* \rightarrow 0$), and to spend

$$E_{1,2}^* = \frac{(1+r)r}{(1+r)^2}$$

when they identify a female that has mated (1), or will mate again (2).

6. BIOLOGICAL EVIDENCE

The above models make both intra- and interspecific predictions about male strategies. The parameters q and r are fixed for a given species, hence their variation in a given model predicts changes across species in which males have the same information. However, within a species, a given model predicts how males respond when they encounter different sperm competition risk contexts, i.e. the intraspecific variation.

There is widespread comparative evidence that average investment in sperm production increases with the level of sperm competition across species. This pattern has been described across diverse taxa in studies which employ a variety of means to quantify the relationship between sperm production and sperm competition (table 1). Recent studies of phenotypic plasticity provide evidence also for similar patterns between different populations within species (He & Tsubaki 1992; Gage 1995; table 1). With few exceptions (e.g. Heske & Ostfield 1990; see, also, Brown *et al.* 1995), these comparative and population studies support the prediction that where sperm competition approximates to some form of raffle, mean relative ejaculate expenditure increases with level of sperm competition. The present paper generates new predictions related to loaded raffles; these should now be tested in comparative studies.

As predicted (Parker 1990a,b), studies of individual variation in ejaculate expenditure within populations suggest a pattern of increased investment in sperm production by males mating consistently in a disadvantaged role with respect to sperm competition and/or experiencing consistently elevated sperm competition risk (e.g. Stockley & Purvis 1993; Gage *et al.* 1995). Theoretical analyses presented here predict intraspecific ejaculate variation: males are expected to adjust the size of their ejaculate at given matings, investing more where the risk of competition is higher, depending on the loading between roles (figures 2, 3). Evidence suggests that males can vary ejaculate size in response to locally perceived risk of sperm competition as revealed by various cues (table 2). For example, the presence of one or more rivals prior to or during mating may be used to indicate future and/or past risk of sperm competition, leading to an increase in the number of sperm ejaculated (Gage & Baker 1991; Gage 1991; Gage & Barnard 1996). The type of cue used to assess risk is likely to vary according to species-specific mating patterns. For example, where males commonly guard or consort with females before copulation, the time spent guarding may be a more reliable indicator of 'past' risk than the presence of rival males, and evidence suggests that sperm numbers may vary with this cue (Baker & Bellis 1989; Bellis *et al.* 1990).

Where males neither congregate around or guard females prior to copulation, female mating status may be a more reliable index of sperm competition risk. Males of some species can assess female mating status and may adjust their ejaculate size accordingly. Indian meal moth males, *Plodia interpunctella*, do not respond to the presence of rivals but instead respond directly to the amount of sperm within the female, delivering larger ejaculates where the sperm competition level is higher (Cook & Gage 1995). Paradoxically, male wartbiters, *Decticus verrucivorus*, deliver more sperm to virgins (Wedell 1992) than to mated females. Males sometimes avoid transferring sperm to mated females that offer very poor prospects: such cases are usually easy to interpret. Male 13-lined ground squirrels (*Spermophilus tridecemlineatus*) suffer decreasing paternity gains with time after a first male's copulation. After a critical delay time (matching the predicted optimum), they reject females (Schwagmeyer & Parker 1990). In the fly *Cyrtodiopsis whitei*, the spermatophore acts as a temporary mating plug and second males avoid transferring sperm to mated females (Lorch *et al.* 1993), as do male bowl and doily spiders, where first male sperm precedence is almost complete (Austad 1984).

Direct assessment of female mating status may not always be a reliable index of sperm competition risk, particularly where there is sexual conflict over remating decisions. Simmons *et al.* (1994) found evidence that previously mated female bushcrickets, *Requena verticalis*, disguise their mating status to avoid male discrimination. Such concealment may be a common female response to sexual conflict over avoidance of sperm competition (Stockley 1997). Where female cues are generally unreliable or difficult to assess, males may instead make use of their own mating

Table 1. *Relationships between investment in sperm production and level of sperm competition: (a) across species and (b) between populations*

taxonomic level	measure of sperm production	measure of sperm competition	relationship: + = positive (supports theory); – = negative (against theory)	source
<i>(a) between species</i>				
mammals				
great apes	testes mass, ejaculate volume, sperm density	copulation frequency	+ species with high copulation frequency have relatively large testes and high sperm reserves	Short 1979
all primates	relative testes mass	mating system	+ species with multi-male mating systems have relatively larger testes than those with monogamous or single-male mating systems	Harcourt <i>et al.</i> 1981 Harvey & Harcourt 1984
	relative testes mass, ejaculate quality (volume, sperm number and motility)	mating system	+ species with multi-male mating systems have relatively larger testes than those with single-male systems and produce ejaculates with higher sperm motility and more motile sperm	Møller 1988a
all mammals	relative testes mass	mating system	+ species with multi-male mating systems have relatively larger testes than those with single-male (monogamous or polygynous) systems	Kenagy & Trombulak 1986
	daily sperm production rate, sperm reserves (number in epididymes)	relative testes size	+ species with relatively large testes have higher daily sperm production rates and higher sperm reserves than those with relatively small testes	Møller 1989
ungulates	relative testes mass	mating system	+ polyandrous species have relatively larger testes than monandrous species	Ginsberg & Rubenstein 1990
voles	relative testes length	mating system	– both promiscuous and monogamous species have relatively large testes compared to polygynous species	Heske & Ostfield 1990
strepsirrhine primates	relative testes volume	mating system	+ / – species with multi-male and solitary-male mating systems have relatively larger testes than pair-living species	Kappeler 1997
bats	relative testes mass	social group size	+ relative testes size increases with social group size	Hosken 1997
birds	relative testes mass, ejaculate quality (volume, sperm concentration, sperm number)	mating system copulation frequency	+ / – polygynous species have relatively larger testes than monogamous species (regardless of copulation frequency), and species with relatively large testes produce more sperm per ejaculate	Møller 1988b
	relative testes mass	female copulation rate	+ relative testes size increases with female copulation rate	Møller 1991
amphibians				
frogs	relative testes mass	mating system	+ species with multi-male mating systems have relatively large testes	Jennions & Passmore 1993
fishes	gonosomatic index; sperm number in stripped ejaculates	sperm competition rank	+ relative testes size and sperm number in stripped ejaculates increases with sperm competition intensity rank	Stockley <i>et al.</i> 1997
insects				
butterflies	mass and production rate of ejaculates	female mating frequency	+ polyandrous species produce larger ejaculates than monandrous species and are able to produce sperm and accessory substances at a greater rate	Svård & Wiklund 1989
	relative testes size	female mating frequency	+ relative testes size increases with female mating frequency	Gage 1994
<i>(b) between populations</i>				
insects				
armyworm <i>Pseudaletia separata</i>	spermatophore size	population density	+ males reared at high larval density produce larger spermatophores	He & Tsubaki 1992
Indian meal moth <i>Plodia interpunctella</i>	relative testes volume; sperm number	population density	+ males reared at high larval density invest more in testes and sperm production	Gage 1995

Table 2. Examples of ejaculate variation in response to perceived risk of sperm competition

risk of sperm competition	cue	response: + =positive (supports theory — = negative (against theory)	source
(i) from future and/or past meetings			
flour beetle <i>Tenebrio molitor</i>	presence of male rival	+ increased sperm number	Gage & Baker 1991
Mediterranean fruit fly <i>Ceratitis capitata</i>	presence of male rival	+ increased sperm number	Gage 1991
wartbiter <i>Decticus verrucivorus</i>	female mating status	—larger spermatophores to virgins than to previously mated females	Wedell 1992
Indian meal moth <i>Plodia interpunctella</i>	presence of male rival	0 no response	Cook & Gage 1995
decorated field cricket <i>Gryllobates suppicans</i>	presence of male rival(s)	+ increased sperm number in relation to number of rivals	Gage & Barnard 1996
house cricket <i>Acheta domesticus</i>	presence of male rival(s)	+ increased sperm number in relation to number of rivals	Gage & Barnard 1996
(ii) from past matings			
humans <i>Homo sapiens</i>	time spent with female prior to copulation	+ increased sperm number in relation to time spent apart from partner prior to copulation	Baker & Bellis 1989
rat <i>Rattus norvegicus</i>	time spent with female prior to copulation	+ increased sperm number with females not previously guarded by the copulating male	Bellis <i>et al.</i> 1990
Indian meal moth <i>Plodia interpunctella</i>	amount of sperm in female storage organs	+ increased sperm number in relation to amount of previous males sperm in storage	Cook & Gage 1995
small white butterfly <i>Pieris rapae</i>	male mating status	+ increased sperm number in second spermatophore produced (when more chance of encountering previously mated females)	Cook & Wedell 1996

status as a reference point for likely risk of sperm competition. Male butterflies (*Pieris rapae*) produce spermatophores with large numbers of sperm during their second copulation, when they are more likely to encounter previously mated females (Cook & Wedell 1996).

In addition to the direct manipulations of ejaculate size with perceived risk of sperm competition listed (table 2), behavioural responses such as variation in the frequency or timing of copulation may also lead to ejaculate variation. Male Rocky Mountain bighorn sheep, *Ovis canadensis canadensis*, perform frequent 'retaliatory' copulations with guarded females immediately after forced copulation attempts by rival males, increasing the total number of sperm transferred where perceived sperm competition risk is high (Hogg 1988). Male zebra finches (*Taeniopygia guttata*) vary the timing of their copulations to ejaculate more sperm under situations of high sperm competition risk. This is achieved by performing extra-pair copulations (associated with high sperm competition risk), when the number and quality of sperm in reserve for ejaculation are highest (Birkhead *et al.* 1995).

This work was supported by NERC grant GR3/9264. We are indebted to David Zeh and to an anonymous reviewer for their help in improving the paper.

REFERENCES

- Austad, S. N. 1984 Evolution of sperm priority patterns in spiders. In *Sperm competition and the evolution of animal mating systems* (ed. R. L. Smith), pp. 223–249. London: Academic Press.
- Baker, R. R. & Bellis, M. A. 1989 Number of sperm in human ejaculates varies in accordance with sperm competition theory. *Anim. Behav.* **37**, 867–869.
- Ball, M. A. & Parker, G. A. 1996 Sperm competition games: external fertilization and 'adaptive' infertility. *J. Theor. Biol.* **180**, 141–150.
- Ball, M. A. & Parker, G. A. 1997 Sperm competition games: inter- and intra-species results of a continuous external fertilization model. *J. Theor. Biol.* **186**, 459–466.
- Ball, M. A. & Parker, G. A. 1998a Sperm competition games: energy dependence and competitor numbers in the continuous external fertilization model. *IMA J. Math. Appl. Med. Biol.* (In the press.)
- Ball, M. A. & Parker, G. A. 1998b Sperm competition games: a general approach to risk assessment. (In preparation.)
- Bellis, M. A., Baker, R. R. & Gage, M. J. G. 1990 Variation in rat ejaculates consistent with the kamikaze-sperm hypothesis. *J. Mamm.* **71**, 479–480.
- Birkhead, T. R. & Parker, G. A. 1997 Sperm competition and mating systems. In *Behavioural ecology: an evolutionary approach*, 4th edn (ed. J. R. Krebs & N. B. Davies), pp. 121–145. Oxford: Blackwell.
- Birkhead, T. R., Fletcher, F., Pellat, E. J. & Staples, A. 1995 Ejaculate quality and the success of extra-pair copulations. *Nature* **377**, 422–423.
- Brown, L., Shumaker, R. W. & Downhower, J. F. 1995 Do primates experience sperm competition? *Am. Nat.* **146**, 302–306.

- Cook, P. A. & Gage, M. J. G. 1995 Effects of risks of sperm competition on the numbers of eupyrene and apyrene sperm ejaculated by the moth *Plodia interpunctella* (Lepidoptera: Pyralidae). *Behav. Ecol. Sociobiol.* **36**, 261–268.
- Cook, P. A. & Wedell, N. 1996 Ejaculate dynamics in butterflies: a strategy for maximizing fertilization success? *Proc. R. Soc. Lond. B* **263**, 1047–1051.
- Gage, M. J. G. 1991 Risk of sperm competition directly affects ejaculate size in the Mediterranean fruit fly. *Anim. Behav.* **42**, 1036–1037.
- Gage, M. J. G. 1994 Associations between body size, mating pattern, testis size and sperm lengths across butterflies. *Proc. R. Soc. Lond. B* **258**, 247–254.
- Gage, M. J. G. 1995 Continuous variation in reproductive strategy as an adaptive response to population density in the moth *Plodia interpunctella*. *Proc. R. Soc. Lond. B* **261**, 25–30.
- Gage, M. J. G. & Baker, R. R. 1991 Ejaculate size varies with sociosexual situation in an insect. *Ecol. Entomol.* **16**, 331–337.
- Gage, A. R. & Barnard, C. J. 1996 Male crickets increase sperm number in relation to competition and female size. *Behav. Ecol. Sociobiol.* **38**, 349–353.
- Gage, M. J. G., Stockley, P. & Parker, G. A. 1995 Effects of alternative mating strategies on characteristics of sperm production in the Atlantic salmon (*Salmo salar*): theoretical and empirical investigations. *Phil. Trans. R. Soc. Lond. B* **350**, 391–399.
- Ginsberg, J. R. & Rubenstein, D. I. 1990 Sperm competition and variation in zebra mating behavior. *Behav. Ecol. Sociobiol.* **26**, 427–434.
- Harvey, P. H. & Harcourt, A. H. 1984 Sperm competition, testes size, and breeding systems in primates. In *Sperm competition and the evolution of animal mating systems* (ed. R. L. Smith), pp. 589–600. Orlando: Academic Press.
- Harcourt, A. H., Harvey, P. H., Larson, S. G. & Short, R. V. 1981 Testis weight, body weight, and breeding system in primates. *Nature* **293**, 55–57.
- He, Y. & Tsubaki, Y. 1992 Variation in spermatophore size in the armyworm, *Pseudaletia separata* (Lepidoptera: Noctuidae) in relation to rearing density. *Appl. Entomol. Zool.* **27**, 39–45.
- Heske, E. J. & Ostfield, R. S. 1990 Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. *J. Mamm.* **71**, 510–519.
- Hogg, J. T. 1988 Copulatory tactics in relation to sperm competition in Rocky Mountain bighorn sheep. *Behav. Ecol. Sociobiol.* **22**, 49–59.
- Hosken, D. J. 1997 Sperm competition in bats. *Proc. R. Soc. Lond. B* **264**, 385–392.
- Jennions, M. D. & Passmore, N. I. 1993 Sperm competition in frogs: testis size and a 'sterile male' experiment on *Chiromantis xerampelina* (Rhacophoridae). *Biol. J. Linn. Soc.* **50**, 211–220.
- Kappeler, P. M. 1997 Intrasexual selection and testis size in strepsirrhine primates. *Behav. Ecol.* **8**, 10–19.
- Kenagy, G. J. & Trombulak, S. C. 1986 Size and function of mammalian testes in relation to body size. *J. Mamm.* **67**, 1–22.
- Lorch, P. D., Wilkinson, G. S. & Reillo, P. R. 1993 Copulation duration and sperm precedence in the stalk-eyed fly *Cyrtodiopsis whitei* (Diptera: Diopsidae). *Behav. Ecol. Sociobiol.* **32**, 303–311.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.
- Møller, A. P. 1988a Testis size, ejaculate quality and sperm competition in birds. *Biol. J. Linn. Soc.* **33**, 273–283.
- Møller, A. P. 1988b Ejaculate quality, testes size and sperm production in primates. *J. Hum. Evol.* **17**, 479–488.
- Møller, A. P. 1989 Ejaculate quality, testes size and sperm production in mammals. *Funct. Ecol.* **3**, 91–96.
- Møller, A. P. 1991 Sperm competition, sperm depletion, paternal care and relative testis size in birds. *Am. Nat.* **137**, 882–906.
- Parker, G. A. 1982 Why are there so many tiny sperm? Sperm competition and the maintenance of two sexes. *J. Theor. Biol.* **96**, 281–294.
- Parker, G. A. 1984a Sperm competition and the evolution of animal mating strategies. In *Sperm competition and the evolution of animal mating systems* (ed. R. L. Smith), pp. 1–60. London: Academic Press.
- Parker, G. A. 1984b The producer/scrounger model and its relevance to sexuality. In *Producers and scroungers: strategies of exploitation and parasitism* (ed. C. J. Barnard), pp. 127–153. London: Croom Helm.
- Parker, G. A. 1990a Sperm competition games: raffles and roles. *Proc. R. Soc. Lond. B* **242**, 120–126.
- Parker, G. A. 1990b Sperm competition games: sneaks and extra-pair copulations. *Proc. R. Soc. Lond. B* **242**, 127–133.
- Parker, G. A. 1993 Sperm competition games: sperm size and number under adult control. *Proc. R. Soc. Lond. B* **253**, 245–254.
- Parker, G. A. 1998 Sperm competition and the evolution of ejaculates: towards a theory base. In *Sperm competition and sexual selection* (ed. T. R. Birkhead & A. P. Møller). London: Academic Press. (In the press.)
- Parker, G. A. & Begon, M. E. 1993 Sperm competition games: sperm size and number under gametic control. *Proc. R. Soc. Lond. B* **253**, 255–262.
- Parker, G. A., Ball, M. A., Stockley, P. & Gage, M. J. G. 1996 Sperm competition games: assessment of sperm competition intensity by group spawners. *Proc. R. Soc. Lond. B* **263**, 1291–1297.
- Shapiro, D. Y. & Giraldeau, L. A. 1996 Mating tactics in external fertilizers when sperm is limited. *Behav. Ecol.* **7**, 19–23.
- Short, R. V. 1979 Sexual selection and component parts, somatic and genital selection, as illustrated by man and the great apes. *Adv. Stud. Behav.* **9**, 131–158.
- Simmons, L. W., Llorens, T., Schinzig, M., Hosken, D. & Craig, M. 1994 Sperm competition selects for mate choice and protandry in the bushcricket, *Requena verticalis* (Orthoptera: Tettigoniidae). *Anim. Behav.* **47**, 117–122.
- Stockley, P. 1997 Sexual conflict resulting from adaptations to sperm competition. *Trends Ecol. Evol.* **12**, 154–159.
- Stockley, P. & Purvis, A. 1993 Sperm competition in mammals: a comparative study of male roles and relative investment in sperm production. *Funct. Ecol.* **7**, 560–570.
- Stockley, P., Gage, M. J. G., Parker, G. A. & Møller, A. P. 1997 Sperm competition in fishes: the evolution of relative testes size and ejaculate characteristics. *Am. Nat.* **149**, 933–954.
- Svärd, L. & Wiklund, C. 1989 Mass and production rates of ejaculates in relation to monandry/polyandry in butterflies. *Behav. Ecol. Sociobiol.* **24**, 395–402.
- Schwagmeyer, P. L. & Parker, G. A. 1990 Male mate choice as predicted by sperm competition in thirteen-lined ground squirrels. *Nature* **348**, 62–64.
- Warner, R. R., Shapiro, D. Y., Marconato, A. & Petersen, C. W. 1995 Sexual conflict: males with the highest mating success convey the lowest fertilization benefits to females. *Proc. R. Soc. Lond. B* **262**, 135–139.
- Wedell, N. 1992 Protandry and mate assessment in the wart-biter *Decticus verrucivorus* (Orthoptera: Tettigoniidae). *Behav. Ecol. Sociobiol.* **31**, 301–308.
- Zeh, J. A. & Zeh, D. W. 1996a The evolution of polyandry. I. Intra-genomic conflict and genetic incompatibility. *Proc. R. Soc. Lond. B* **263**, 1711–1717.
- Zeh, J. A. & Zeh, D. W. 1996b The evolution of polyandry. II. Postcopulatory defences against genetic incompatibility. *Proc. R. Soc. Lond. B* **264**, 69–75.

Received 25 April 1997; accepted 16 June 1997

As this paper exceeds the maximum length normally considered for publication in *Proceedings B*, the authors have agreed to make a contribution towards production costs.