

Sperm competition games between related males

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Three sperm competition games against relatives are examined. In the first, a male has no information at the time of mating as to whether or not his ejaculate will face sperm competition from a related or unrelated male. Sperm expenditure increases with overall sperm competition risk q and declines with the probability ρ that the competitor shares the same allele for sperm expenditure. In the second game, males have almost perfect information: they 'know' whether there will be sperm competition and, if so, whether this involves a related or unrelated male. Sperm expenditure is reduced by a factor ρ when competing with a relative. In the third game, males 'know' when they compete with relatives, but have no information for other matings whether they will face sperm competition from unrelated males. A male without information expends less on his ejaculate than a male competing with a close relative if the overall risk of sperm competition is low, but more if the overall risk is high. The average relative ejaculate expenditure is the same in all three games so that, if this determines testis size, data is required only on the overall sperm competition risk, the probability of competing with a relative and the average ρ in order to perform comparative analyses.

Keywords: sperm competition; evolutionarily stable strategies; games between relatives

1. INTRODUCTION

Sperm competition games (reviewed by Parker 1998) are evolutionary models which predict evolutionarily stable strategy (ESS) sperm allocation strategies under sperm competition (competition between the sperm from rival ejaculates) (Parker 1970). An assumption of all models investigated has been that competing males are unrelated. The present paper examines cases where rival males are relatives. This is not uncommon in certain groups. For instance, in felids, lion brothers commonly hold prides of females (Packer & Pusey 1982) and cheetah brothers typically form coalitions in order to gain matings (Caro & Collins 1987). Sperm competition between brothers can also occur in birds, for example in the Tasmanian native hen *Tribonyx mortierii*, two brothers commonly share a sister and help to rear her offspring (Maynard Smith & Ridpath 1972). In the insects, Hymenoptera such as fig wasps often compete with brothers for matings with their sisters, which emerge from the same fig (e.g. Hamilton 1979). Varying levels of sib competition for mates are found in parasitoid Hymenoptera in species which have been examined in the context of local mate competition as tests of sex ratio theory (e.g. see Charnov 1982).

2. MODELLING APPROACH

To investigate the effects of relatedness between competing males on sperm allocation at mating, I followed the logic of 'risk models' in sperm competition games (Parker *et al.* 1997). I first give a brief introduction to the analytical technique used in several previous papers (reviewed by Parker 1998), which is then modified to analyse sperm competition games between relatives.

Let the probability that a given female mates twice be q and that she mates once be $(1 - q)$. The possibility that

a female mates more than twice for a particular set of eggs is ignored, which is a fair approximation if q is not too large. This has been called the risk model in which sperm competition forms a relatively rare risk to distinguish it from the 'intensity' model in which there are typically several males in competition for each set of eggs (Parker *et al.* 1996). A male allocates effort (i) to his ejaculate (which determines the expected value of each mating) and (ii) to gaining matings (which determines the number of matings he achieves). The models assume a fixed budget for total reproductive expenditure, so that there is a trade-off between these two components (see Parker 1998).

In the present paper, sperm are assumed to have a fixed mass and to be associated with a fixed amount of seminal fluid, so that the number of sperm transferred at mating determines the ejaculate expenditure. The cost of an ejaculate containing s units of sperm is Ds , where the constant D is the cost of one unit of sperm including the cost of the associated seminal fluid.

Consider a population in which males play the ESS sperm allocation, s^* units of sperm per ejaculate. Let $W(s, s^*)$ be the personal fitness of a rare mutant male that deviates by playing $s \neq s^*$ against a population of competitors playing s^* . Following previous analyses (Parker 1990, 1998a), personal fitness is assumed to be the number of matings achieved, $n(s, s^*)$, multiplied by the expected value of each mating, $v(s, s^*)$:

$$W(s, s^*) = n(s, s^*) \times v(s, s^*). \quad (1)$$

This multiplicative approach is preferred (see Ball & Parker 2000) to an alternative additive approach recently suggested by Mesterton-Gibbons (1999a, b).

Each male has a fixed energy budget of R units and the average cost of obtaining each mating (finding a female, etc.) is C units. Let $\langle s \rangle$ and $\langle s^* \rangle$ be the average sperm allocations by a mutant and by an ESS player, respectively.

The ESS number of matings per male is thus

$$n(s^*, s^*) = R / (C + D\langle s^* \rangle), \tag{2}$$

and a mutant playing $s \neq s^*$ achieves

$$n(s, s^*) = R / (C + D\langle s \rangle) \tag{3}$$

matings.

In the absence of sperm competition, maximum fertility is assumed to be achieved with minimal sperm ($s \rightarrow 0$) as in previous analyses (see Parker 1998; but see Mesterton-Gibbons 1999a). Assuming that sperm compete after the ‘loaded raffle’ (Parker 1990a), the fertilization gains to two males occupying roles 1 and 2 are

$$\frac{s_1}{s_1 + rs_2} \tag{4}$$

for the male in role 1, and

$$\frac{rs_2}{s_1 + rs_2} \tag{5}$$

for the male in role 2, where r represents the competitive loading of sperm in role 1 relative to sperm in role 2. Typically, roles 1 and 2 may be the order of mating, so that r is the loading due to the effect of the timing asymmetry on fertilization. It is assumed that a given male occurs in each role with equal probability (Parker 1990a). Roles can be non-random, which requires a different analysis (Parker 1990a). For convenience we take $0 \leq r \leq 1$, so that role 2 is defined as the disfavoured role (Parker 1990a).

The two competing males are relatives with probability α and unrelated with probability $(1 - \alpha)$ and ρ signifies the coefficient of relatedness between the related males (*sensu* Hamilton 1964), e.g. 0.5 for full-sibs and 0.25 for half-sibs. It should be noted that r has generally been used as the term for the coefficient of relatedness in the kin selection literature. It is stressed that r is used here as the raffle loading factor in order to retain uniformity with several other papers on sperm competition games.

A basis for incomplete information and risk assessment in sperm competition games has already been developed (Parker *et al.* 1997; Ball & Parker 1998). Three games are examined here. They differ in the information available to a male when mating. In game 1, on meeting a female males have no information whether or not an ejaculate will face sperm competition from a related or unrelated male. In game 2, males have almost perfect information: they ‘know’ when there will be sperm competition and, if so, whether this involves a related or unrelated male. However, there is no knowledge of the exact relationship to the related competitor (e.g. whether the competitor is a half-sib or a full-sib). In game 3, when relatives compete, the relationship is ‘known’. However, some matings occur without information: then the ejaculate may face either no sperm competition or sperm competition from an unrelated male.

3. GAME 1: NO INFORMATION

Here males have no information about the risk or nature of sperm competition at the time of mating. Their ejaculation strategy is tuned by the average probabilities of q and α for the population. Biologically, such

circumstances may occur when matings typically involve the presence of just a single male and female and there are no obvious cues available to indicate whether a female has mated previously or will mate again before fertilization occurs.

Two rather different analytical approaches give the same ESS solution. First, consider an approach based on population genetics (e.g. Parker & Macnair 1978) or personal fitness (e.g. Grafen 1979). Fitness is measured here in terms of the replication of a rare dominant mutant allele for ejaculating $s \neq s^*$. Being rare, s occurs in a focal male that is heterozygous, carrying alleles for s and s^* . The focal male achieves a number of matings given by equation (3) and gains an expected number of progeny carrying the mutant allele from each mating:

$$v(s, s^*) = 0.5[(1 - q)g_0 + q(1 - \alpha)g_{s, s^*} + q(1 - \rho)\alpha g_{s, s^*} + q\rho\alpha g_{s, s}] / (1 + q), \tag{6}$$

in which the g terms are the relative numbers of offspring expected from the different types of mating, assuming that roles 1 and 2 are occupied randomly (with equal probability) by the mutant male. To explain equation (6), remember that a given male expects $2q$ matings involving sperm competition (q in each of the roles 1 and 2) for every $(1 - q)$ matings without sperm competition, giving $(1 + q)$ matings in all. Thus, on $(1 - q)$ occasions, the focal male gains all the available offspring and $g_0 = 1.0$. On $q\rho\alpha$ occasions, the focal male occurs in each of roles i and j in competition with a relative carrying the same mutant allele, who also plays $s \neq s^*$, thus

$$g_{s, s} = \left[\frac{s}{s + rs} + \frac{rs}{rs + s} \right] = 1.0. \tag{7}$$

When the focal male meets an unrelated male (on $q(1 - \alpha)$ occasions) or a relative which does not carry the mutant allele (on $q(1 - \rho)\alpha$ occasions) he plays against s^* sperm in each of roles i and j and, hence,

$$g_{s, s^*} = \left[\frac{s}{s + rs^*} + \frac{rs}{rs + s^*} \right]. \tag{8}$$

Note that, when $s = s^*$, the whole of the square bracketed term in equation (6) summates to 1.0 and the value $v(s^*, s^*) = 0.5 / (1 + q)$. The 0.5 in equation (6) occurs because only half the focal male’s progeny will carry the labelled allele. However, the constant $0.5 / (1 + q)$ in equation (6) is of little consequence, being lost when we differentiate the product of equations (3) and (6) and set

$$\left. \frac{\partial W(s, s^*)}{\partial s} \right|_{s=s^*} = 0 \tag{9}$$

in order to obtain the ESS in terms of s^* (Parker 1990a,b). As with other sperm competition game solutions (see Parker 1998), the ESS is most conveniently expressed in terms of the proportion of the total reproductive effort that is expended on the ejaculate:

$$E^* = \frac{Ds^*}{C + D\langle s^* \rangle} = 2q(1 - \rho\alpha) \left(\frac{r}{(1 + r)^2} \right). \tag{10}$$

Expenditure E^* increases linearly with q , the probability that females mate twice. The effect of the loading

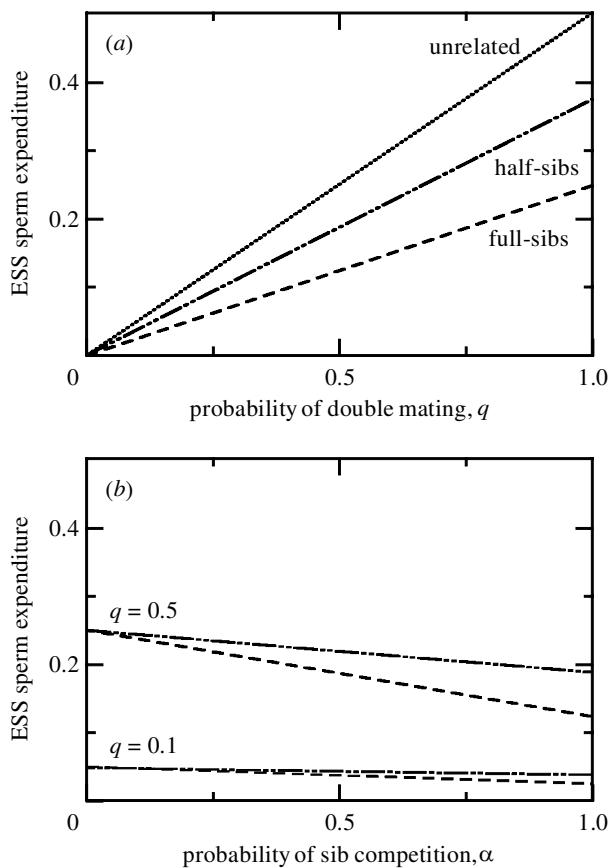


Figure 1. ESS sperm expenditure E^* predicted for game 1. (a) Expenditure in relation to q , the probability of double mating in a population, for a fair raffle ($r = 1.0$). Dotted line, all competing males are unrelated; dashed-dotted line, all competing males are half-sibs; dashed line, all competing males are full-sibs. (b) Expenditure in relation to α , the probability that the two competing males are brothers under two conditions of overall risk, $q = 0.1$ and $q = 0.5$. Dashed-dotted line, all competing males are half-sibs; dashed line, all competing males are full-sibs.

in the raffle (term $r/(1+r)^2$) remains the same in this and the next two analyses (see also Parker *et al.* 1997). The term $\rho\alpha$ measures the probability that the focal allele competes against the same mutant allele. If there is no sperm competition between relatives ($1 - \rho\alpha = 1.0$) and the ESS is as previously reported by Parker *et al.* (1997), E^* declines linearly as $\rho\alpha$ increases. Sperm competition between full brothers (rather than half brothers) will reduce the ESS sperm allocation at given values of q and r . If sperm competition is always between sibs ($\alpha = 1.0$), for fair raffles ($r = 1.0$) E^* becomes $q/4$ for competing full-sibs ($\rho = 0.5$) and $3q/8$ for half-sibs ($\rho = 0.25$) (see figure 1a). This compares with $q/2$ for non-sibs (Parker *et al.* 1997). Increasing the probability α that relatives compete decreases E^* ; figure 1b shows this decrease at two values of q (0.1 and 0.5) for half- and full-sibs.

An alternative approach to the ESS comes from a direct application of Hamilton's (1964) inclusive fitness rule. Hines & Maynard Smith (1979) termed this the 'standard' ESS to distinguish it from the approach above, which they termed a 'Grafen' ESS. Here we take a focal mutant 'a' playing s which sometimes competes with its brother 'b' playing s^* and find the ESS by differentiating

$$W(s, s^*) = W_a(s, s^*) + \rho W_b(s^*, s) \\ = n_a(s, s^*) \times v_a(s, s^*) + \rho n_b(s^*, s) \times v_b(s^*, s), \quad (11)$$

where $W(s^*, s)$ is the fitness of a male playing s^* against a competitor playing s . This gives the same result as equation (10). Mesterton-Gibbons (1996) showed that the conditions for a standard ESS are neither necessary nor sufficient for a Grafen ESS in games among kin, though for an interior ESS (of the type found in this paper) they will often, for clearly identified reasons, yield the same result, as in the present paper.

4. GAME 2: RISK KNOWLEDGE AND KIN RECOGNITION

Here a male 'knows' whether his ejaculate will face sperm competition and, if so, whether he competes with a relative or non-relative. The game relates to, for example, a social species with kin recognition, in which a male knows whether only he will mate with a given female and whether a second group member will compete and, if so, whether the competitor is a relative or non-relative.

A male mating with a female which will not mate again ($1 - q$ occasions) should deliver an arbitrary minimum ejaculate (see Parker *et al.* 1997). We therefore seek strategy I , which is the conditional ESS for ejaculating s_u^* when competing against an unrelated male and s_b^* when competing with a brother (or other relative).

First, consider a rare mutant, which deviates by playing $s_u \neq s_u^*$ against unrelated males; against brothers he does not deviate from the ESS s_b^* . His ejaculate expenditure will be the arbitrary minimum (which we take as equal to zero) on $(1 - q)$ occasions and on $2q$ occasions expends either s_u (with probability $1 - \alpha$) or s_b^* (with probability α). Thus, his average ejaculate expenditure across these $(1 + q)$ occasions is

$$\langle s_u \rangle = 2q[(1 - \alpha)s_u + \alpha s_b^*]/(1 + q) \quad (12)$$

and

$$n(s_u, I) = \frac{R}{C + D\langle s_u \rangle} \quad (13)$$

following equation (3).

Remember that, when playing against a relative ($q\alpha$ occasions), the mutant does not deviate and, hence, plays s_b^* . Thus, the gain is $1/(1 + r)$ offspring in role 1 and $r/(1 + r)$ offspring in role 2, so that the sum (one mating in each role) is $g_{s_b^*, s_b^*} = 1.0$. The expected value of a mating now becomes

$$v(s_u, I) = 0.5[(1 - q)g_0 + q(1 - \alpha)g_{s_u, s_u} + q\alpha g_{s_b^*, s_b^*}]/(1 + q), \quad (14)$$

where $g_0 = 1.0$; and when playing against a non-relative, the gain is

$$g_{s_u, s_u} = \left[\frac{s_u}{s_u + r s_u^*} + \frac{r s_u}{r s_u + s_u^*} \right]. \quad (15)$$

Thus, at the ESS, $v(I, I) = 0.5/(1 + q)$ as before.

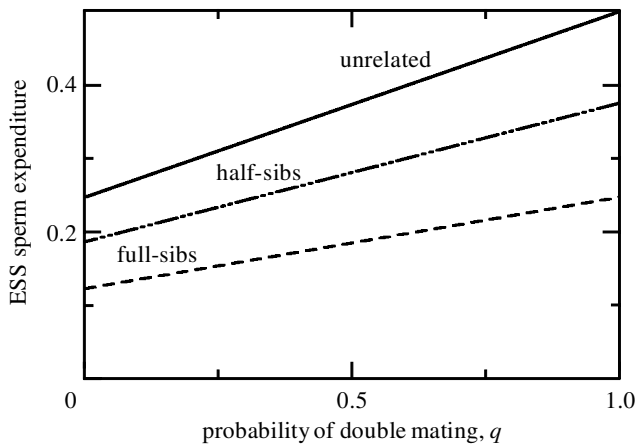


Figure 2. ESS sperm expenditures E_u^* and E_b^* predicted for game 2 in relation to q , the probability of double mating in a population, for a fair raffle ($r = 1.0$). The expenditure E_u^* with unrelated males (continuous line) and the expenditure E_b^* with related males (broken lines). Two cases of expenditure with related males are shown: dashed–dotted line, all competing males are half brothers; dashed line, all competing males are full brothers.

We obtain the ESS expenditure s_u^* as before by differentiating the product of equations (13) and (14) and evaluating at s_u^* . This gives the result that

$$E_u^* = \frac{Ds_u^*}{C + D\langle I \rangle} = (1 + q) \left(\frac{r}{(1 + r)^2} \right), \tag{16}$$

which corresponds to the ESS for the same game but where all sperm competition occurs between unrelated males (Parker *et al.* 1997), but note that $\langle I \rangle$ will differ for the two cases.

We derive the ESS for s_b^* in a parallel manner. The relevant equations for a mutant deviating by playing $s_b \neq s_b^*$ become

$$\langle s_b \rangle = 2q[(1 - \alpha)s_u^* + \alpha s_b] / (1 + q) \tag{17}$$

and

$$v(s_b, I) = 0.5[(1 - q)g_0 + q(1 - \alpha)g_{s_u^*, s_u^*} + q(1 - \rho)\alpha g_{s_b, s_b^*} + q\rho\alpha g_{s_b, s_b}] / (1 + q), \tag{18}$$

where $g_0 = g_{s_b, s_b} = 1.0$ and

$$g_{s_b, s_b^*} = \left[\frac{s_b}{s_b + r s_b^*} + \frac{r s_b}{r s_b + s_b^*} \right]. \tag{19}$$

Deriving the ESS in the usual way gives

$$E_b^* = \frac{Ds_b^*}{C + D\langle I \rangle} = (1 + q)(1 - \rho) \left(\frac{r}{(1 + r)^2} \right). \tag{20}$$

Comparing equation (20) with equation (16), the ESS expenditure when competing with a relative is $(1 - \rho)$ times smaller than that when competing with a non-relative (see figure 2). Relatedness again clearly reduces ejaculate expenditure and equation (20) converges towards equation (16) as the average relatedness between the competing males declines towards $\rho = 0$. Note that both s_u^* and s_b^* are dependent on α through the term $\langle I \rangle$.

5. GAME 3: COMPETITION FROM RELATIVES KNOWN AND NO INFORMATION ON RISK FROM NON-RELATIVES

This is a special case in which the sperm competition between relatives is always ‘known’ to both players. However, a sperm competition risk also applies between non-related males, though there is no information about this risk. Biologically, this could apply to a species in which related males (e.g. brothers) sometimes collaborate in holding harems or guarding single females and where each may mate with a given female in the presence of the other. Males may also sometimes mate with females singly, but have no knowledge of the sperm competition risk from an unrelated male at the time of mating.

We again seek strategy I , which is the conditional ESS for ejaculating s_n^* when there is no relative in competition and s_b^* when competing against a relative.

Solving first for s_n^* , a mutant deviating by playing $s_n \neq s_n^*$ faces no sperm competition on $(1 - q)$ occasions and faces sperm competition from an unrelated male on $2q(1 - \alpha)$ occasions, though he cannot detect which of these will occur. On $2q\alpha$ occasions he plays against a relative and expends s_b^* , as does his brother. His average ejaculate expenditure across $(1 + q)$ occasions is thus

$$\langle s_n \rangle = [(1 + q)s_n + 2q(1 - \alpha)s_n + 2q\alpha s_b^*] / (1 + q) \tag{21}$$

and the expected value of a mating is

$$v(s_n, I) = 0.5[(1 - q)g_0 + q(1 - \alpha)g_{s_n, s_n^*} + q\alpha g_{s_b, s_b^*}] / (1 + q), \tag{22}$$

where $g_0 = g_{s_b, s_b^*} = 1.0$ and

$$g_{s_n, s_n^*} = \left[\frac{s_n}{s_n + r s_n^*} + \frac{r s_n}{r s_n + s_n^*} \right]. \tag{23}$$

The ESS becomes

$$E_n^* = \frac{Ds_n^*}{C + D\langle I \rangle} = \left(\frac{2q(1 + q)(1 - \alpha)}{1 + q - 2q\alpha} \right) \left(\frac{r}{(1 + r)^2} \right). \tag{24}$$

Note that, as for equation (10), if $\alpha = 0$ (no competition with relatives), equation (24) reduces to the ESS for zero information with random mating (equation (9) of Parker *et al.* (1997)). Also note that, since $(1 + q)(1 - \alpha) < (1 + q - 2q\alpha)$ when $q < 1.0$, the ESS (equation (24)) is less than for zero information with random mating when $\alpha > 0$; increasing α reduces expenditure.

Solving next for s_b^* , a mutant deviating by playing $s_b \neq s_b^*$ has $\langle s_b \rangle$ as in equation (21) but with s_n^* replacing s_n and s_b replacing s_b^* . The term $v(s_b, I)$ remains the same as in game 2. The ESS also becomes the same as in game 2:

$$E_b^* = \frac{Ds_b^*}{C + D\langle I \rangle} = (1 + q)(1 - \rho) \left(\frac{r}{(1 + r)^2} \right) \tag{25}$$

and the value of $\langle I \rangle$ is also the same (see § 6).

Figure 3 shows the two ESS sperm allocations E_b^* (broken lines) and E_n^* (continuous curves) at various parameter values, but all for a fair raffle ($r = 1.0$). E_b^* decreases with the probability ρ that the related competitor carries the same s_b allele (see equation (25)). If we set $\rho = 0$, the model can be interpreted in terms of competition purely between non-relatives, in which E_b^*

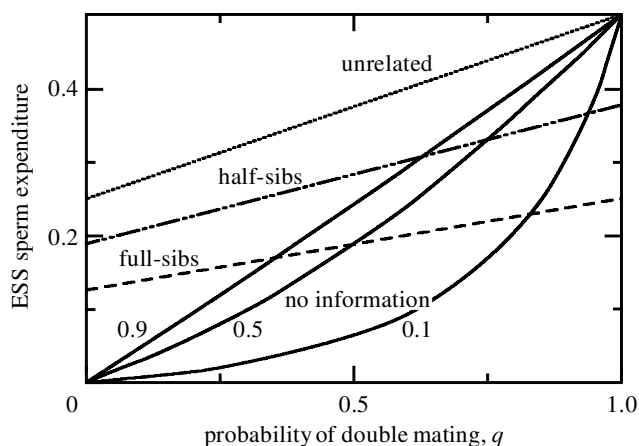


Figure 3. ESS sperm expenditures E_n^* and E_b^* predicted for game 3 in relation to q , the probability of double mating in a population, for a fair raffle ($r = 1.0$). The expenditure E_n^* without information (continuous lines) representing α (the probability that two competing males are relatives) = 0.1, 0.5 and 0.9 and the expenditure E_b^* with related males (broken lines). Three cases of expenditure with 'related' males are shown: dotted line, all competing males are unrelated; dashed-dotted line, all competing males are half brothers; dashed line, all competing males are full brothers.

defines the strategy when sperm competition is 'known' and E_n^* is the strategy in the absence of information about risk. Again, s_b^* is dependent on α through term $\langle I \rangle$.

Expenditure with no information, i.e. E_n^* , is shown at $\alpha = 0.1$, $\alpha = 0.5$ and $\alpha = 0.9$ in figure 3. As α increases, 'known' instances of competition increase, so that the occasions where two males mate without information, i.e. $q(1 - \alpha)$, decreases. Thus at given q , E_n^* decreases with α (see figure 3).

Note that, when mating in the presence of a relative, the ESS expenditure at low q exceeds that when mating without information, but at high q the reverse applies (figure 3).

6. DISCUSSION

It is of interest to estimate the average expenditure at the ESS in the three games. In game 1, the average expenditure is given by equation (10), since s^* sperm is ejaculated on all occasions. In game 2, E_n^* is ejaculated with probability $2q(1 - \alpha)/(1 + q)$ and E_b^* with probability $2q\alpha/(1 + q)$. In game 3, E_n^* occurs with probability $[(1 - q) + 2q(1 - \alpha)]/(1 + q)$ and E_b^* again with probability $2q\alpha/(1 + q)$. Using these probabilities, it is easy to show that the average ejaculate expenditure $\langle I \rangle$ is the same in both games 2 and 3 and again equal to equation (10). So for species with given values of q , α and ρ , the average ejaculate expenditure and, hence, possibly also the average testis size, should be independent of the information rules of the game, at least over the three games examined.

However, a difficulty with making biological predictions from the type of model presented here is that, across species, the probability of sperm competition q often covaries with the probability that sibs compete, i.e. α . Thus, in those felids where brothers collaborate to attain matings, the probability of sperm competition is probably

higher than for a comparable species in which sibs do not compete, because for the latter species the likelihood q that two males mate with the same female is much reduced. Similar effects may apply for Hymenoptera subject to local mate competition. An analysis of testis size across such species would be interesting, particularly where q and α can be estimated.

An interesting discontinuity at $q = 0$ occurs between the alternative expenditure strategies in games 2 and 3, as found previously in the games analysed by Parker *et al.* (1997). The explanation for this is that, in some cases (equations (10) and (24)), at the time of mating sperm competition is uncertain and the risk declines to zero as $q \rightarrow 0$, thus males make arbitrary minimum investment. In other cases (equations (16), (20) and (25)), the mating male has information that sperm competition is certain even though this is an extremely rare occurrence and, hence, expends considerable sperm.

The reason that ESS expenditure typically continues to increase as q increases is best understood by considering the definition of E_i^* , which is the ejaculate cost Ds_i^* , divided by the sum of the cost of obtaining the mating and the cost of the average ejaculate, $C + D\langle I \rangle$. At $q \rightarrow 0$, the average ejaculate cost is zero and $E_i^* \rightarrow Ds_i^*/C$. For all cases, as q increases, $D\langle I \rangle$ increases, because the probability of known or unknown sperm competition risk increases. If, at the time of mating, sperm competition is uncertain, Ds_i^* increases from zero with q , so that E_i^* must increase with q . The increase in E_i^* is less easy to understand for the cases where sperm competition is already certain at the time of mating. This arises because, when there is sperm competition, the expected value of a mating v increases with sperm expenditure. As q increases, pay-offs under sperm competition become a relatively more important component of fitness. Thus, when 'no-risk' mates are common, it pays to economize on sperm in risk matings to obtain as many no-risk matings as possible. However, when sperm competition is prevalent, it pays to expend more sperm to increase the value of each mating, rather than to conserve effort for searching for rare no-risk females.

Ball & Parker (1998) examined the implications of such discontinuities when animals have limited assessment abilities and make mistakes in assessment. This can lead, with only tiny amounts of information, to large changes in sperm expenditure, something which must be considered when analysing data. For instance, at low q in game 3, if cues associated with no information change towards cues hinting of competition (with kin or otherwise), a large increase in expenditure may occur even though the information content of the change is only very marginal.

One possibility arising from this analysis is that, if a male is mating with a sister, this may increase the likelihood that he will face sperm competition from a brother (sib mating may correlate with low population mixing). Thus, assuming that he can detect relatedness, he should reduce his sperm allocation relative to matings with unrelated females. Experimental results in which females appear to prefer sperm from unrelated males are therefore open to the interpretation that the effect is due to strategic sperm allocation by males rather than to sperm selection by the female (e.g. Wilson *et al.* 1997; Stockley 1999). This can be ruled out for Stockley's (1999) results,

since the sperm numbers were counted and found not to differ between males that were related and those that were unrelated to the female.

In none of the cases analysed here has an active role for the female been considered. There is increasing evidence for sperm selection or 'cryptic female choice' (see the recent reviews in Birkhead & Møller (1998)). It is not immediately obvious how sperm selection by females might influence the predictions, since it is not clear how female interests are affected by male expenditures. If it is in female interests to disfavour sperm from related males, then where competition between brothers correlates positively with matings with sisters (see above), females may actively reduce sperm numbers when detecting matings from kin. However, any such reductions should affect both competitors equally (each loses a given sperm with the same probability) in all the present models, which include only competition between identical males (related or unrelated), not competition between males of different relatedness to the female. Thus none of the pay-offs or the ESSs would be affected.

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