Spermicide by females: what should males do?

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The female reproductive tract can be particularly aggressive towards ejaculates, often leading to the death of large numbers of sperm. It has been suggested that males can respond to these actions by investing more in sperm and donating larger ejaculates. Such counteractions may lead to arms races, which can have significant implications for the mating system. In a series of simple models we first show that arms races are not necessarily supported: in fact, sperm killing may even favour no change or reductions in sperm allocation. Second, we identify a simple mechanistic rule for sperm killing that determines whether an arms race or sperm reduction will be favoured. Which of these responses is favoured by selection depends on whether a certain number, or proportion, of sperm are killed. When a specific number is killed, larger investment in sperm is favoured and when a specific proportion is killed, no change or lower investment in sperm is favoured. Both of these mechanisms are biologically plausible.

Keywords: sperm competition; spermicide; arms race; sexual selection; male–female conflict; sperm phagocytosis

1. INTRODUCTION

Traditionally, sperm competition has been treated as a male–male conflict, with females being an inert arena in which the conflict occurs. However, more recently, experimental evidence has shown that the manipulating role of females may be substantial and can have a dramatic effect on the outcome of sperm-competition games, and this has attracted consideration in models (Birkhead & Møller 1993; Gowaty 1994; Parker 1998).

In the extreme case, it has been suggested that females may mate with a number of males and then select the sperm that will be used to fertilize their eggs (cryptic female choice; Eberhard 1996) though the evidence for this has often (but not always) been flawed (Birkhead 1998). If cryptic female choice predominates over sperm competition, we would expect very little sperm to be transferred, since ejaculating more sperm does not translate into much more paternity and resources are therefore probably better invested in antagonistic characters used to overcome the female's sperm-selection mechanism.

One method females use to make such selection is through spermicide, be this through discarding received sperm ('sperm dumping'; Ginsberg & Rubenstein 1990; Birkhead & Møller 1992; Baker & Bellis 1993; Birkhead *et al.* 1993; Eberhard 1996; Elgar 1998; Gomendio *et al.* 1998), through digesting sperm (Bauer 1998; Michiels 1998; Westheide 1999) or through phagocytosis of spermatozoa (Birkhead *et al.* 1993; Bishop 1996; Gomendio *et al.* 1998; Koehler *et al.* 1998; Westheide 1999). It is also conceivable that males have evolved to produce large quantities of sperm in order to confuse or otherwise confound females' cryptic systems of selection. In these cases spermicide may possibly evolve as a counter-adaptation, to facilitate sperm selection. In addition, spermicide may benefit the female simply by providing a valuable nutrient source (Calow *et al.* 1979; Walker 1980).

Regardless of the function, spermicide is ubiquitous in animals and the female reproductive tract is commonly exceptionally hostile towards received sperm (Birkhead *et al.* 1993; but see Olsson & Madsen 1998). The question we ask here is how male sperm-allocation patterns should alter in response to sperm killing by females. That is, we analyse one specific evolutionary response to spermicide that males may make, namely to alter the number of sperm ejaculated.

Simmons & Parker (1989) suggested that if female consumption of sperm affects each male equally, this might not affect the optimal number of sperm produced by males, since it need not change the relative gains to each male at fertilization. Hence, unless the first male's ejaculate is significantly eroded before the second male mates, no change may be expected. However, Birkhead *et al.* (1993) considered the same problem and suggested that spermicide by females could lead to an arms race in which escalated amounts of sperm are produced and females eliminate more of the received sperm. Greeff & Michiels (1999a) made a similar argument for hermaphrodites, which from further work (Greeff & Michiels 1999b) could also be generalized to gonochorists.

Which of these predictions will generally be true? By studying a number of simplified models we try to identify conditions that determine the outcome of these sperm-competition games. It turns out that an arms race is not necessarily supported and, in certain cases, spermicide can in fact lead to a reduction in male sperm allocation. The outcome depends on the mode of spermicide.

2. A BASIC GAME

An early approach to sperm allocation under sperm competition is that of Parker (1982), whose approach we follow here. Let a proportion p of males' matings involve sperm competition with one other male; note that where q is the proportion of females that mate twice, $p = 2q/(1 + q)$ (Parker 1998). Let the proportion of resources invested in

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sperm be s . If each unit of resources leads to D sperm, it means that sD spermatozoa are produced. Further, assume that all males have the same amount of resources available and that sperm of the two males compete in a fair raffle (Parker 1990). Hence, if a mutant male transfers s resource units of sperm in a population where other males transfer the evolutionarily stable allocation s^* , then the proportion of offspring fertilized by the mutant is $s/(s + s^*)$ (notice that D cancels out). The male's fitness per mating is thus proportional to this fraction. We assume that investment made in sperm production is at the cost of an alternative investment, such as finding mates and/or 'persuading' them to mate (see Parker 1998). A simple way to represent such a trade off is by the function $(1 - s)/(1 - s^*)$. Fitness through this alternative investment decreases linearly as more resources are invested in sperm. We can then combine the two parts by multiplication to obtain an expression for the fitness (w) of the mutant male:

$$w = \frac{1 - s}{1 - s^*} \left[p \frac{s}{s + s^*} + 1 - p \right]. \tag{1}$$

To find the evolutionarily stable allocation to sperm, s^* , we use the standard technique of differentiating the fitness function to the mutant strategy (s), setting the mutant and population strategies equal ($s = s^*$) in the derivative and setting the derivative equal to zero. By solving for s in this equation we obtain the evolutionarily stable strategy (ESS; Maynard Smith 1982). Note that optimality has to be checked by inspecting the second derivative. In this fashion we find that the optimal investment in sperm in the basic model is

$$s^* = \frac{P}{4 - p} \tag{2}$$

(Parker 1982, 1990), which is 1/3 if p is 1.

There are various ways in which spermicide can be incorporated into this basic model. We make a distinction depending on whether a fixed number or fixed proportion of sperm are killed since these two scenarios give qualitatively different ESS solutions.

3. NUMERIC (SUBTRACTION) MODELS

(a) Continuous spermicide

Supposing that in addition to the basic model we now have the complication that the female kills a certain number of sperm per unit time. Since the two males mate at different times, different numbers of their sperm will be killed by the time of fertilization. If amounts h_1 of the first male's sperm and h_2 of the second male's sperm are killed between the moments of ejaculation and fertilization ($h_1 > h_2$) then we can adjust the basic model accordingly:

$$w = \frac{1 - s}{1 - s^*} \left[\frac{p}{2} \left(\frac{s - h_1}{s - h_1 + s^* - h_2} + \frac{s - h_2}{s - h_2 + s^* - h_1} \right) + 1 - p \right]. \tag{3}$$

The factor of 2 in the denominator arises since a male has equal probability of being first or second to mate. The ESS investment can be found to be

$$s^* = \frac{(2 - p)(h_1 + h_2) + p}{4 - p}, \tag{4a}$$

giving

$$s^* = \frac{1 + h_1 + h_2}{3} \tag{4b}$$

when $p = 1$, and the same results as the basic model when $h_1 = h_2 = 0$. From equations (4) it is clear that as more sperm are killed (whether females increase the number of killed sperm by killing at a higher rate or by delaying their oviposition longer after mating) h_1 and h_2 increase, and males' sperm allocations will increase.

(b) Sperm 'safe haven'

In this scenario a fixed, equal number of each male's sperm are killed, for instance on their way to a 'safe haven'. Once safety is reached, the sperm partake in the fair raffle. This is just a special case of the previous model in that $h_1 = h_2 = h$, and the ESS is simply

$$s^* = \frac{(2 - p)2h + p}{4 - p}, \tag{5a}$$

giving

$$s^* = \frac{1 + 2h}{3} \tag{5b}$$

when $p = 1$. As above, investment in sperm should be increased as the killing becomes more severe. This will allow an arms race to be established where escalation in sperm killing favours escalation in sperm allocation.

(c) Selective spermicide

Now consider a case where a female, when mated to two males, kills h of only the less-preferred male's sperm. Assuming that each male is equally likely to be in the role of more- or less-preferred male and that neither male 'knows' which role he will occupy, the fitness equation can be adjusted to

$$w = \frac{1 - s}{1 - s^*} \left[\frac{p}{2} \left(\frac{s - h}{s - h + s^*} + \frac{s}{s + s^* - h} \right) + 1 - p \right], \tag{6}$$

giving the optimal sperm allocation of

$$s^* = \frac{(2 - p)h + p}{4 - p}. \tag{7}$$

Again, unequal but fixed 'subtractive' spermicide, even though it leads to an inequality in paternity between the males, leads to an increase in sperm allocation.

4. PROPORTIONAL (MULTIPLICATIVE) MODELS

(a) Continuous spermicide

Imagine a situation similar to that of § 3(a), except that in each time unit in the female tract rather than fixed numbers of sperm being killed, fixed proportions of sperm are killed. Let the remaining sperm at the time of fertilization be proportions m_1 and m_2 (for the first and

second male, respectively), $m_1 < m_2$. For simplicity, assume now that all matings involve sperm competition between just two males ($p = 1.0$). The fitness function can now be written as

$$w = \frac{1-s}{1-s^*} \cdot \frac{1}{2} \cdot \left(\frac{sm_1}{sm_1 + s^*m_2} + \frac{sm_2}{sm_2 + s^*m_1} \right). \quad (8)$$

The ESS sperm allocation can be found as

$$s^* = \frac{2m_1m_2}{m_1^2 + 4m_1m_2 + m_2^2}. \quad (9)$$

In this model, sperm allocation is reduced as the difference between m_1 and m_2 increases. If spermicide is proportionately increased in both ejaculates, i.e. m_1 and m_2 are multiplied by a constant factor, c , smaller than 1, then equation (9) remains unaltered since the constant cancels out. On the other hand, if spermicide is increased or decreased so that the difference between m_1 and m_2 increases, then sperm allocation will decrease. When equal proportions of sperm are killed, m cancels out of the equation and $s^* = 1/3$, as in the basic model.

A second, more explicit, approach to continuous sperm death can be formulated thus. Suppose that spermicide occurs both during movement of sperm from the site of insemination to the sperm store, involving a probability of death per sperm of k_a per time unit, and during storage in the sperm store, with probability of death per sperm k_b . There is a time-delay, d , between the two matings (male 1 is the first to mate, male 2 the second). Let the average time to reach the sperm store be t_a for each ejaculate and let fertilization occur at time T after the first copulation ($T > t_a$). The time spent by male 1's sperm in storage before fertilization is $t_b = T - t_a$. If s_1 sperm are ejaculated by the first male and s_2 by the second, the numbers of sperm present in the store at fertilization time T from each will be

$$s_1(T) = s_1 e^{-k_a t_a - k_b t_b}, = 0 \text{ if } T < t_a \text{ from male 1;} \quad (10a)$$

$$s_2(T) = s_2 e^{-k_a t_a - k_b (t_b - d)}, = 0 \text{ if } T < t_a + d, \text{ from male 2} \quad (10b)$$

and hence the relative fertilization success, assuming that both have sperm present in the sperm store at the time of fertilization ($T > t_a + d$), can be shown to be

$$\frac{s_1}{s_1 + s_2 e^{k_b d}} \text{ to male 1,} \quad (11a)$$

$$\frac{s_2 e^{k_b d}}{s_1 + s_2 e^{k_b d}} \text{ to male 2} \quad (11b)$$

(Parker 1998). The effect of spermicide on pay-offs therefore depends on the total sperm killed ($k_b d$) between the two matings. For each surviving sperm from male 1, there will be $e^{k_b d}$ surviving sperm from male 2 at the time of fertilization, assuming both have ejaculated equal sperm numbers. Spermicide simply becomes a special case of the loaded raffle (Parker 1990; see also Parker *et al.* 1997), with the raffle loading factor $r = e^{k_b d}$. The ESS for this game, making the same assumptions as before, but assuming that all matings involve two males ($p = 1$) is

$$s^* = \frac{2r}{1 + 4r + r^2} \quad (12)$$

(Parker 1990). Note that equation (12) is formally equivalent to equation (9) if we let $rm_1 = m_2$, where r is a constant of proportionality, equivalent to the loading factor in the raffle. Thus optimal sperm allocation, s^* , is at a maximum when $r = 1$ and decreases as r increases. In other words, sperm allocation is reduced as d and/or k_b increases. Hence, higher rates of sperm death (increases in k_b) lead to a reduction in sperm allocation. Such a situation will thus not support an arms race; rather it will generate sperm reduction. When $d = 0$, i.e. no time-delay between matings, and hence no differential effect on the two ejaculates, the model gives the same result as equation (9) and leads to $s^* = 1/3$. Hence, no matter what proportion of sperm is killed, if males are not affected differentially, they will not alter their ejaculate size at all. As d increases the inequality increases leading to less and less investment in sperm.

(b) Sperm 'safe haven'

This question has been partly answered in §4(a). When the same proportions of the two males' sperm are killed before they are stored in a safe reservoir, the spermicide will not lead to any change in sperm allocation. This is just a special case of the models above, and we can explain it in two ways. First, notice how spermicide *en route*, k_a , in the previous model cancelled out of equations (10). Second, the same happens to k_b when $d = 0$. As a result, spermicide of equal proportions of ejaculates, no matter how severe, will not lead to any change in sperm allocation.

(c) Selective spermicide

Here we consider a case where a female actively and selectively kills more of one male's sperm than the other, hence enhancing the paternity of the favoured male. This is just a special case of the models in §4(a), where we found that as the absolute difference between m_1 and m_2 increased (e.g. by increasing d), sperm allocation decreased. Hence, favouritism under proportional spermicidal rules leads to the complete opposite to under subtraction: males should decrease sperm allocation when females selectively kill the sperm of certain males. However, we stress that this conclusion relates to the case where all males have equal chances of being favoured or disfavoured, i.e. where these roles are random *sensu* Parker (1990).

5. DISCUSSION

Obtaining these widely differing predictions using models in which the mechanism of spermicide is entered only slightly differently is rather alarming. It must also be possible to produce a myriad of other alternatives and more complicated interactions, which make it hard to draw general conclusions.

Why does the dichotomy between additive and multiplicative models exist? The fact that sperm allocation escalates with h is obvious in the subtractive model. A male must always pay the fixed cost h for sperm killed, but every sperm produced above this will count fully in the fair raffle. So as h increases, s^* must increase to offset the costs of spermicide. In the proportionate model, all sperm from a given male are discounted equally, however

many of them are produced. The more that the sperm in one role are disfavoured, the easier it becomes to make gains in the raffle in the favoured role; effectively sperm competition is less intense, favouring reduced expenditure.

Hence, when females kill a fixed number of sperm, rather than a fixed proportion, the general rule is that increased spermicide will lead to increased sperm production and an arms race will be possible. In fact, in these models it is theoretically possible for the arms race to continue until males invest almost all their 'reproductive' energy in sperm. This can have a dramatic effect on the mode of sexual selection, leading to economies in expenditure on direct male-male competition to allow increased sperm allocation as a result of sperm competition under aggressive spermicide by females. Biologically, spermicide might be subtractive when the female's mechanism for sperm eradication can cope with only a given number of sperm at a given time. Candidate examples might include a part of each ejaculate being taken into a fixed-volume receptacle for spermicide or a fixed population of phagocytes in the female tract quickly becoming saturated over the time-period of exposure to each ejaculate.

On the other hand, in cases where females kill a proportion rather than a number of sperm, the general picture seems to be that an arms race will not evolve. Indeed, a reduction in sperm numbers is predicted; in the end this may be balanced by females' need to ensure fertilization. Biologically, there are plausible mechanisms that would result in proportionate reductions of ejaculates. Purely passive loss with a fixed instantaneous death or loss rate per sperm (Lessells & Birkhead 1990) would generate the multiplicative case. It would also apply with active spermicide by a population of phagocytes in the female tract where each phagocyte kills a sperm in negligible 'handling time', so that increased sperm numbers do not reduce the fixed death rate per sperm.

A response in terms of sperm number is not the only recourse males have to spermicide. Males might also evolve adaptations to neutralize or circumvent females' actions and we list a few possibilities. First, males may produce larger, more resistant or faster sperm to minimize the chemical attacks on them. The large variation in sperm size and morphology between and within species is often interpreted as a result of male-male competition (Simmons & Siva-Jothy 1998) but may well be the result of male-female arms races. Second, males may produce ejaculates that neutralize some of the females' attacks with mammalian ejaculates being a possible example (Gomendio *et al.* 1998). Third, males may produce a spermatophore that protects the sperm (Vreys *et al.* 1997; Baur 1998). Finally, they may try to bypass aggressive female reproductive tracts by using hypodermic impregnation techniques (Baur 1998; Michiels 1998; Michiels & Newman 1998).

In conclusion, the type of mechanism by which females kill sperm (multiplicative or subtractive) in a given system is critical in determining whether there will be escalated or reduced sperm allocation by males.

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