

Sperm competition games: optimal sperm allocation in response to the size of competing ejaculates

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Sperm competition theory predicts that when males are certain of sperm competition, they should decrease sperm investment in matings with an increasing number of competing ejaculates. How males should allocate sperm when competing with differently sized ejaculates, however, has not yet been examined. Here, we report the outcomes of two models assuming variation in males' sperm reserves and males being faced with different amounts of competing sperm. In the first 'spawning model', two males compete instantaneously and both are able to assess the sperm competitive ability of each other. In the second 'sperm storage model', males are sequentially confronted with situations involving different levels of sperm competition, for instance different amounts of sperm already stored by the female mating partner. In both of the models, we found that optimal sperm allocation will strongly depend on the size of the male's sperm reserve. Males should always invest maximally in competition with other males that are equally strong competitors. That is, for males with small sperm reserves, our model predicts a negative correlation between sperm allocation and sperm competition intensity, whereas for males with large sperm reserves, this correlation is predicted to be positive.

Keywords: ejaculate size; genetic algorithm; sexual selection; sperm competition intensity; sneaker; strategic sperm allocation

1. INTRODUCTION

Sperm competition is a strong selective force that has been shown to affect male behaviour, physiology and morphology, as well as many important life-history traits (Parker 1970; Birkhead & Møller 1998; Simmons 2001). Sperm competition occurs when sperm from more than one male compete for fertilizations (Parker 1998). One interesting aspect of sperm competition that has received much theoretical and empirical interest regards the proportion of reproductive resources that male should allocate to sperm production, and how much of a male's present sperm reserves should be spent in specific matings (for reviews, see Parker 1998; Simmons 2001; Wedell *et al.* 2002). If sperm compete numerically, a male's immediate fertilization success will be a monotonically increasing function of sperm number in the ejaculate. Yet, it is fair to assume that sperm production bears some costs (Pitnick & Markow 1994a; Olsson *et al.* 1997). Therefore, one can also assume that an increased size of the ejaculate will act negatively on either a male's future mating success or the sperm reserves available for future matings, or both (Nakatsuru & Kramer 1982; Pitnick & Markow 1994b; Warner *et al.* 1995; Danielsson 2001). Because the expected gain, in terms of gained fertilizations per invested sperm amount, is likely to be different between matings, males are expected to invest their sperm strategically (e.g. Parker 1990b, 1998; Parker *et al.* 1996, 1997; Reinhold *et al.* 2002; Wedell *et al.* 2002; Engqvist & Reinhold 2006). One of the most important factors that will have profound

effects on male optimal sperm allocation is the expected number of sperm that the focal male's sperm will be competing against in the subsequent raffle for fertilizations. Hitherto, two different approaches have been used to model the range of sperm competition encountered by males: the 'risk' and the 'intensity' models (e.g. Parker *et al.* 1996, 1997; Engqvist & Reinhold 2006). The risk model mimics the situation in species with a low level of sperm competition, where females may mate either once or, with a certain probability (risk), twice. This model predicts that if males are able to distinguish between matings with a high and low sperm competition risk, they should always allocate a larger amount of their present sperm reserves to the matings with a high risk of sperm competition (Parker 1990b, 1998; Parker *et al.* 1997; but see Engqvist & Reinhold 2006). On the other hand, the intensity model simulates an intense sperm competition in species where males frequently encounter sperm competition and often from more than one ejaculate. The intensity model predicts that if males are certain that sperm competition will occur, they are expected to invest a smaller amount of sperm with an increasing number of competing ejaculates (Parker *et al.* 1996). It is important to bear in mind that in this particular analysis, ejaculates from different males contain an equally large amount of sperm; hence, the sperm competition intensity can be measured as the number of competing ejaculates.

In this study, we will use yet another approach to model a different range of sperm competition intensity that has so far not been analysed theoretically – variation in competing ejaculate size. Males are likely to differ in the amounts of

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sperm resources that they have available for each mating (e.g. Engqvist & Sauer 2001, 2003; Stockley & Seal 2001; Schaus & Sakaluk 2002). This will have two consequences. First, parallel to differences in male sperm reserves, there is likely to be variation in the size of competing ejaculates. This prompts the question of how males should respond to differences in either the size of competing ejaculates or the amount of sperm stored by females from competing males. Second, the size of male sperm reserves will inevitably affect the trade-off between fertilization success in present and future matings, which is the rationale for male strategic allocation. This leads to the problem how male strategic sperm allocation in response to the levels of sperm competition is affected by the size of male sperm reserves.

It is obvious that the number of sperm in a competing ejaculate will influence the pay-off equation that describes fertilization success as a function of sperm expenditure in a mating. It is therefore straightforward to assume that males should change sperm allocation in matings in response to the size of the competing ejaculate. However, the shape of the response function seems far from clear. Using verbal arguments (see Wedell & Cook 1999a), it has been claimed that when the competing sperm amount is large, approaching the size of two or more average ejaculates, the situation might be analogous to the intensity model (Parker *et al.* 1996), with competition between several ejaculates. At this high level, the marginal fitness increase (fertilization probability per sperm) of any additional sperm investment constantly declines (cf. Parker *et al.* 1996). Thus, at a high level of sperm competition, one would expect a negative correlation between the number of competing sperm and the male sperm allocation. In contrast, at a low level of immediate sperm competition, approaching a minute number of competing sperm, an increased sperm investment will only result in a higher degree of competition between self-sperm (i.e. satiation; see also Reinhold *et al.* 2002). Thus, at a low level of sperm competition, one would expect a positive correlation between the size of the competing ejaculate and the optimal sperm allocation of the focal male. In summary, both these arguments infer a maximum sperm allocation at intermediate numbers of competing sperm. However, no attempt has been made to confirm this presumption, and it is not possible to deduce the location of the maximum sperm allocation from these arguments. Furthermore, there are two distinct situations, which require different modelling approaches and possibly different solutions. Either both competing males are able to assess and respond strategically to the expected ejaculate size of the other male prior to mating, or only one male is able to respond to the sperm amount in the other competing ejaculate.

To illustrate the first situation, let us imagine the following situation: in a species with external fertilization, there is a frequent occurrence of sperm competition between two males. However, males differ in their sperm competition capacity, i.e. the magnitude of their present sperm reserves, and are therefore able and expected to deliver ejaculates of different sizes. Furthermore, both males are assumed to perceive not only the presence of the other male at the spawning site, but also the competitive ability of each other. How much sperm should a male allocate to the present mating dependent on the size of his

own and of the competing male's sperm reserve? In this situation, the optimal male strategy will also be affected by the strategy chosen by the competing male. Thus, this is a typical game theory problem (e.g. Maynard Smith 1982).

The other situation will often arise when females store sperm and mate in sequence with different males. In this case, it is conceivable that the mating male may respond to the amount of stored sperm from previous matings. Yet, it seems unlikely that previous males can detect the sperm competition capacity of succeeding males. Therefore, this situation does not demand a game theory approach, but rather a straightforward optimization model will be adequate.

In this study, we use both these approaches to predict optimal male sperm allocation in response to varying competing sperm amount. We use a game theory approach for a 'spawning' situation, where both males are able to assess their competitor and respond strategically. As an extension, we use an optimization model for situations where only the succeeding males are able to respond strategically to the sperm amount transferred by previous males.

2. MATERIAL AND METHODS

(a) *Basic model assumptions*

In both models, we assumed a 'fair raffle' of sperm (Parker 1990a). Thus, the fertilization success (v) of a male allocating a number s of sperm in a mating, where competition with x foreign sperm will follow, is given by:

$$v(s, x) = \frac{s}{s + x}. \quad (2.1)$$

Furthermore, we assumed males to have a limited amount of sperm available, so that an increased amount of sperm allocated to a given mating will negatively affect the number of sperm available for future matings. The exact character of this trade-off was slightly differently shaped for the two different models and will be explained in detail below.

(b) *The 'spawning model': males have information on the sperm competition capacity of their competitors*

We assumed that males differ with respect to their phenotypic state (e.g. condition, size, etc.), and this will translate into a difference in the limited amount of sperm which each male has available for a certain time of the reproductive season. Phenotypic state was assumed to be a discrete variable. Thus, males in state C_i will have the sperm amount R_i available ($i = \{1, 2, \dots, j, \dots\}$; Sumida *et al.* 1990). The relative frequency of males in phenotypic state C_i was assumed to be equal to \tilde{p}_i . Males were assumed to have the mating success N_i depending on their status. Thus, the relative frequency of each phenotype at matings will equal

$$p_i = \tilde{p}_i \frac{N_i}{\bar{N}}, \quad (2.2)$$

where \bar{N} denotes the average mating frequency of all males. In addition, males have to allocate the sperm amount R_i on N_i matings, resulting in an average amount of $r_i = R_i/N_i$ sperm available for each mating.

We assumed that there will be an optimal sperm allocation strategy for each phenotypic state C_i that will determine how much sperm a male in state C_i will spend in a mating competing with a male in state C_j . This amount is denoted by $s_i[j]$. Thus, the sperm allocation strategy s_i of phenotype C_i will be a vector, and its length will equal the number of different phenotypes.

We were now interested in the evolutionarily stable conditional strategy \mathcal{S}^* (cf. e.g. Gross 1996) that will determine how much a male in state C_i will spend on matings in competition with a male in state C_j . This strategy \mathcal{S} is a two-dimensional vector (i.e. matrix) consisting of the different phenotypic strategies, thus $\mathcal{S} = \{\mathbf{s}_1, \mathbf{s}_2, \dots, \mathbf{s}_7, \dots\}$. We denote W_i as the fitness of a male in phenotypic state C_i . The strategy \mathcal{S} will be the evolutionarily stable strategy (ESS) $\mathcal{S}^* = \{\mathbf{s}_1^*, \mathbf{s}_2^*, \dots, \mathbf{s}_i^*, \dots\}$, if, for all i , the inequality $W_i(\mathbf{s}_i^*, \mathcal{S}^*) > W_i(\mathbf{s}_i, \mathcal{S}^*)$ holds, where \mathbf{s}_i indicates a mutant strategy deviating from $\mathbf{s}_i^* \in \mathcal{S}^*$ for any value $\mathbf{s}_i[j] \neq \mathbf{s}_i^*[j]$. At equilibrium, the fitness of a male in phenotypic state C_i with strategy \mathbf{s}_i will equal

$$W_i = \sum_j p_j \frac{\mathbf{s}_i[j]}{\mathbf{s}_i[j] + \mathbf{s}_j^*[i]}, \quad (2.3)$$

provided that the sperm limitation constraint

$$r_i \geq \sum_j p_j \mathbf{s}_i[j], \quad (2.4)$$

is met.

We used a genetic algorithm to estimate the different evolutionarily stable sperm allocation strategies $\mathbf{s}_i^* \in \mathcal{S}^*$ of males. Genetic algorithms are tools used to find optima in complex systems (Holland 1975). They are based on genetic systems and natural evolution (Sumida *et al.* 1990; Mitchell & Taylor 1999), which also means that genetic algorithms can be a very effective search technique to find solutions for game theory problems, such as sperm competition games (e.g. Reinhold *et al.* 2002; Engqvist & Reinhold 2006), in which the optimal strategy of a male will depend on the strategies of other males.

We assumed discrete generations that consisted of seven sets of 70 male strategies each. These different sets of male strategies represent different male phenotypic states. Thus, the phenotypic state of a male can take one of seven different values. In all simulations, 7×70 random allocation strategies ($\mathbf{s}_1, \mathbf{s}_2, \dots, \mathbf{s}_7$) were generated at the beginning of the first generation. Such a strategy comprises seven values ($\mathbf{s}_i[1], \mathbf{s}_i[2], \dots, \mathbf{s}_i[7]$) determining the sperm number a male should allocate in different situations, hence in competition with a male in state $C_j, j = \{1, 2, \dots, 7\}$. The reproductive success of a male with strategy \mathbf{s}_i was calculated using the formulae described above, with the exception that the mean values for each strategy value $\bar{\mathbf{s}}_i[j] = \sum_{m=1}^{70} \mathbf{s}_i[j]_m / 70$ were used instead of $\mathbf{s}_i^*[j]$. Within each set, the 35 most successful male strategies were used to generate the allocation strategies of the next generation. Preliminary strategies were first generated by randomly choosing one of the 35 selected strategies from the previous generation. With a recombination rate of 0.75, one of its strategy values ($\mathbf{s}_i[j]$) was altered by selecting the corresponding value at random from one of the other 35 most successful strategies. This process was repeated 70 times in each of the seven sets to result in 7×70 new strategies.

Following selection and recombination, we randomly selected 5% (mutation rate) of all preliminary strategy values and changed them by randomly adding or subtracting a random number from a uniform distribution (± 0.1). If this process, which was included to simulate mutation, rendered negative values, the respective allocation value was altered to zero. Furthermore, the resulting strategy may not meet the sperm limitation constraint $r_i \geq \sum_j p_j \mathbf{s}_i[j]$. Therefore, the values were rescaled to meet this assumption. Hence, the values of the new strategy $\tilde{\mathbf{s}}_i$ will equal

$$\tilde{\mathbf{s}}_i = \mathbf{s}_i \frac{r_i}{\sum_j p_j \mathbf{s}_i[j]}. \quad (2.5)$$

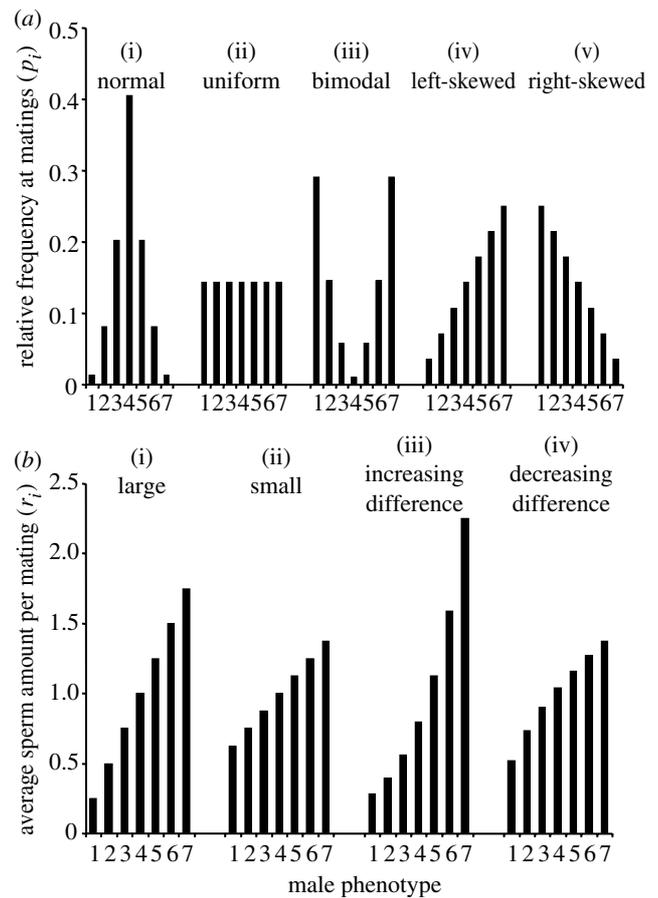


Figure 1. Visualization of the parameter settings in the different simulations. In (a), the different frequency distribution at mating (p_i) is shown. In (b), male's average sperm amount available per mating (r_i) is illustrated. In all simulations, the average sperm amount over all male phenotypes is identical and equals one unit of sperm.

The strategy values now obtained were used to calculate male fitness in the next generation, and so on.

Presumably, the reproductive success of a male will depend not only on its strategy, but also on both the frequency of the different male phenotypes and the variance in sperm competitiveness between the phenotypes. Therefore, we performed simulations assuming various distributions for both r (sperm reserves) and p (frequency at mating). An overview of the different simulation parameters is given in figure 1. We assumed five different distributions of p : (i) 'normal', phenotypes with intermediate sperm reserves are most frequent, (ii) 'uniform', all phenotypes are equally frequent, (iii) 'bimodal', phenotypes with small and ample sperm reserves are equally frequent and intermediate phenotypes are rare, (iv) 'left-skewed', phenotypes with ample sperm reserves are most frequent, and (v) 'right-skewed', phenotypes with small sperm reserves are most frequent (figure 1a). Variance in sperm reserves (r) was simulated in four different ways (figure 1b). Two simulations assumed a linear relation between the phenotypic state and the amount of male sperm reserves, but with a different span between the largest (i) and the smallest (ii) values simulating a small and large variance in male sperm competition ability. In addition, two simulations assumed a nonlinear relation between the phenotypic state and the amount of male sperm reserves: one with an increasing difference (exponential) in sperm reserves between male phenotypes with increasing phenotypic

state (iii) and the other with a decreasing difference (square root) in sperm reserves between males (iv).

Note that in the genetic algorithm, male phenotypes are characterized by r_i and p_i , not by R_i and \tilde{p}_i . This distinction is important when interpreting the results. Males with the largest sperm reserves per mating (r) must not necessarily have the largest total sperm reserves (R). Similarly, the most frequent phenotype (\tilde{p}_i) must not be the most frequent one at mating (p). Both r_i and p_i will be shaped not only by R_i and \tilde{p}_i , respectively, but also from the different mating success of the phenotypes. Thus, with this approach, we avoid making assumptions regarding how phenotypic state affects the mating success.

Generally, the simulations obtained an equilibrium corresponding to the ESS extremely fast (within the first 20 generations). To be on the safe side, we ran all simulations for 500 generations. All simulations were repeated 50 times to calculate mean values and confidence intervals for the different ESS.

(b) The ‘sperm storage model’: males have exact information on the number of competing sperm

In this model, we assumed that a male responds to the number of sperm its own sperm will compete against in the subsequent raffle for fertilizations. However, in contrast to the previous model, the number of competing sperm will not change in response to the male strategy. We assumed that males have a limited amount of sperm (r) available, which have to be allocated on two matings, one immediate and one in the future. In the first mating, males are able to assess the number of competing sperm (x). In the second mating, a male will face a certain amount of sperm (X), which will be a random number from a given known distribution $p(X)$. Thus, the average fitness of a male with sperm amount r , allocating s number of sperm in the first copulation in response to x number of competing sperm, will be

$$W(s, x) = \frac{s}{s+x} + \int_{X_{\min}}^{X_{\max}} p(X) \frac{r-s}{(r-s)+X} dX, \quad (2.6)$$

where $p(X)$ gives the probability density function of X .

Using numeric iterations, we searched for values of s that will maximize the male fitness (W) for given values of x and r , and for different distributions of X . The formula

$$W(s, x) = \frac{s}{s+x} + \sum_{i=X_{\min}}^{X_{\max}} p_i \frac{r-s}{(r-s)+X_i}, \quad (2.7)$$

which is simply the discrete version of equation (2.6), was used to calculate the average fitness of males, allocating s sperm to copulations involving x competing sperm.

For any given $p(X)$, we computed the optimum value of s , $s^*(r, x)$, for several different values of r and x . The values of x were evenly distributed between X_{\min} and X_{\max} . Finally, we had to choose the range of r -values, for which the optimum allocation strategy has to be found. It is reasonable to assume that the realistic variation in male r -values is related to the variation in competing sperm amounts $p(X)$. Yet, males must allocate their sperm over two copulations; therefore, it is realistic to assume that males with sperm reserves $r=2X$ will approximately be as frequent as competing sperm amount X . Therefore, the values describing the sperm reserves of focal males, r , for which we searched the optimum sperm allocation, were evenly distributed between $2 \times X_{\min}$ and $2 \times X_{\max}$.

3. RESULTS

(a) The ‘spawning model’: males have information on the sperm competition capacity of their competitors

Our simulations generated stable and highly repeatable results. The repeatability of single ESS estimates equalled 99.87% ($F_{48,2401} = 40.0 \times 10^3$, $p \ll 0.0001$) in the simulation, with the parameter settings yielding the lowest repeatability. Furthermore, the mean coefficient of variation (s.d./mean) over all simulations was as low as 0.23%. Therefore, here we present mean values only.

The most central result is that the evolutionarily stable sperm allocation strategy will strongly depend on a male’s phenotypic state. In all simulations, the resulting ESS will be to expend most sperm in competition with males belonging to the same phenotypic state (figures 2 and 3) and to spend a decreasing amount of sperm with an increasing difference in competitive ability in relation to the competing male. Thus, males with the smallest sperm reserves per mating should invest maximally in competition with males with equally small sperm reserves and decrease sperm investment with increasing competitor capacity. In contrast, males belonging to the phenotype with the largest sperm reserves should increase sperm investment with increasing capacity of its competitor and invest maximally in competition with equally strong competitors. For intermediate phenotypes, males should increase sperm investment with increasing capacity, reaching a peak in competition with identical males, and decrease investment with increasing competitor capacity.

Assuming different frequency distributions of the various male phenotypes at mating (p_i) did not change this central prediction (figure 2). Yet, subtle changes in sperm allocation pattern are expected. For example, the difference between male phenotypes in their reaction to a certain competitor seems to be much more extreme the less frequent the competitor phenotype is. This becomes evident if one compares the shape of the different ESS curves in figure 2, in particular, the curves describing optima from populations with left- and right-skewed distributions of male phenotypic state (figure 2d,e). Neither did the variance in sperm reserves (r) between male phenotypes change any of the central conclusions. Smaller differences in sperm reserves between competing males simply generated smaller differences in sperm allocation patterns (figure 3), which intuitively makes sense.

(b) The ‘sperm storage model’: males have exact information on the number of competing sperm

As predicted, the number of competing sperm will strongly influence the optimal male sperm allocation to a mating. As in the previous model, optimal sperm allocation will strongly depend upon a male’s own sperm reserves. Thus, the sperm amount of competitive ejaculates at which a male should invest maximally will differ between males with different amounts of sperm available. Analogous to the previous model, males with small sperm reserves (r) should invest maximally in competition with relatively small ejaculates, and then decrease investment with increasing competing ejaculate size (figure 4). In contrast, males with relatively large sperm reserves should generally increase sperm allocation with increasing size of competing ejaculates, reaching a maximum at relatively

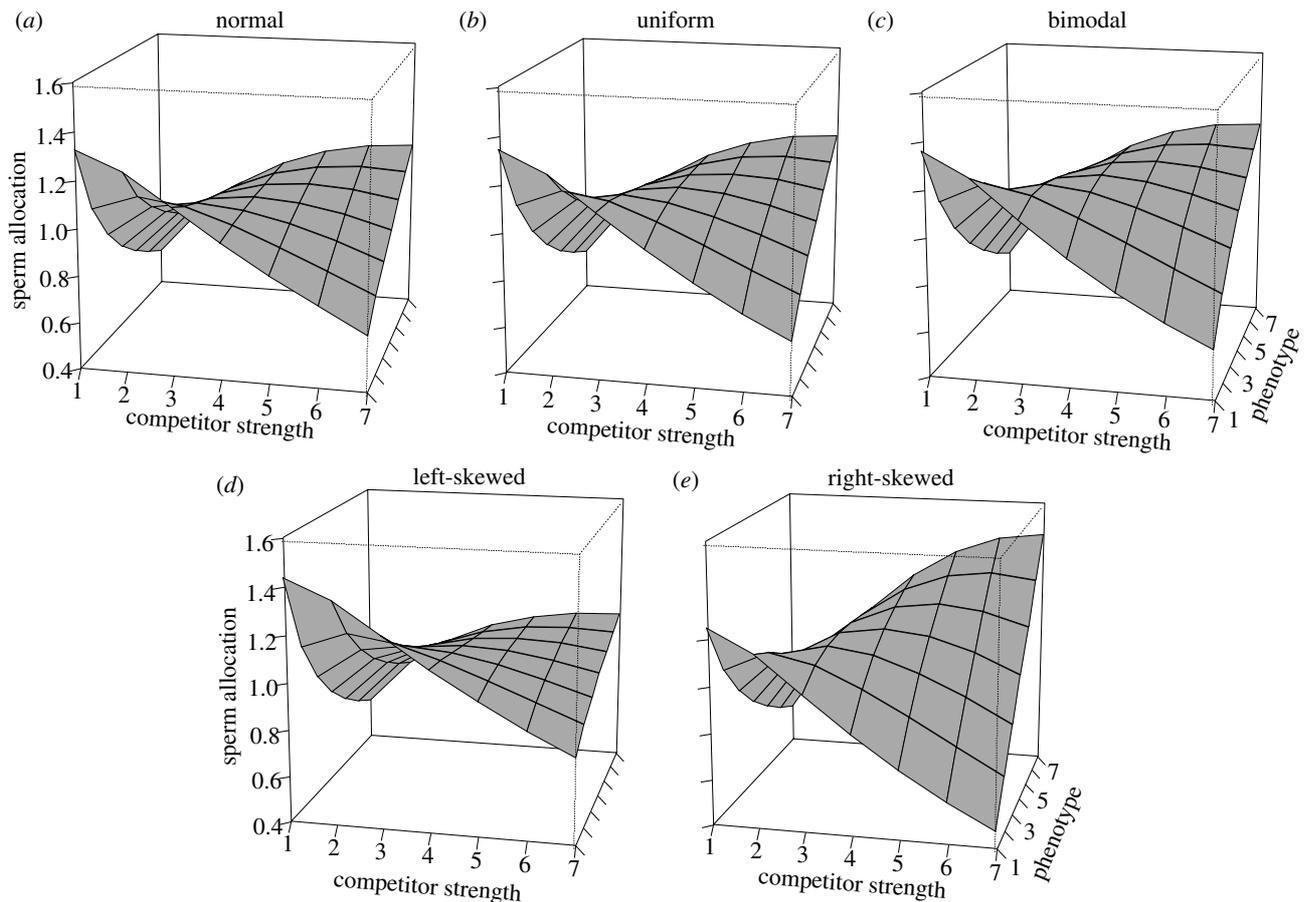


Figure 2. The ESS matrix \mathbf{S}^* describing optimal sperm allocation for different male phenotypes in response to the sperm competition strength of competitors. The label 'phenotype' refers to the phenotypic state of the focal male and the label 'competitor strength' to the phenotype of competitors. 'Sperm allocation' is given as sperm allocated in relation to the average number of sperm allocated per mating for each different phenotype. In all these simulations, large variances in available sperm reserves between male phenotypes (cf. figure 1*b*) were assumed.

high levels of sperm competition (figures 4 and 5). However, for all males, the level of sperm competition yielding maximum sperm allocation roughly equals half the sperm amount in a male's sperm reserve ($r/2$) (figure 5). Thus, as this is the average sperm amount a male expends in each mating, we can conclude that males should expend most sperm when competing against ejaculates that are similar in size to their own average ejaculates. Actually, sperm investment should peak at competition intensities marginally above this level (figure 5), but the difference will only be noteworthy for males with sperm reserves at the extreme upper and lower end of the distribution.

As in the spawning model, reducing the variance in the level of sperm competition simply reduces the variance in sperm allocation response. Furthermore, using frequency distributions other than the normal distribution did not change any of the previous conclusions. These outputs are not presented here, but rendered qualitatively the same results.

4. DISCUSSION

In this study, we used a new approach to model male strategic sperm allocation in response to the level of sperm competition. In our model, males face certain sperm competition from another male's sperm. However, the amount of sperm in competing ejaculates was assumed to

differ. As another extension relative to previous models, we further assumed that males are likely to differ with respect to the size of their sperm reserves. Most importantly, we found that male sperm allocation in response to the intensity of sperm competition will be strongly affected by the amount of sperm a male has available for matings. For males with small or minute sperm reserves, there should be a negative correlation between sperm competition intensity and optimal sperm allocation, whereas for males with ample sperm amounts, this correlation is predicted to be positive (figures 2–4). With respect to these conclusions, the results from our two different models are entirely congruent, although completely different approaches were used.

The spawning model predicts that male sperm expenditure should be greatest in competition with similar males (figures 2 and 3). This prediction is analogous to the outcome of the sperm storage model, which forecasts that males will expend the greatest amount of sperm in competition with ejaculates that equal the average size of their own ejaculates (figure 5). In the original intensity model (Parker *et al.* 1996), all males were assumed to be of equal capacity. Therefore, the predictions from the present study are fully congruent with one of the predictions from the intensity model (Parker *et al.* 1996), namely that males should expend most sperm in competition with exactly one competitor. By our focus on variation in the size of only one competing ejaculate, it has thus been possible to extend

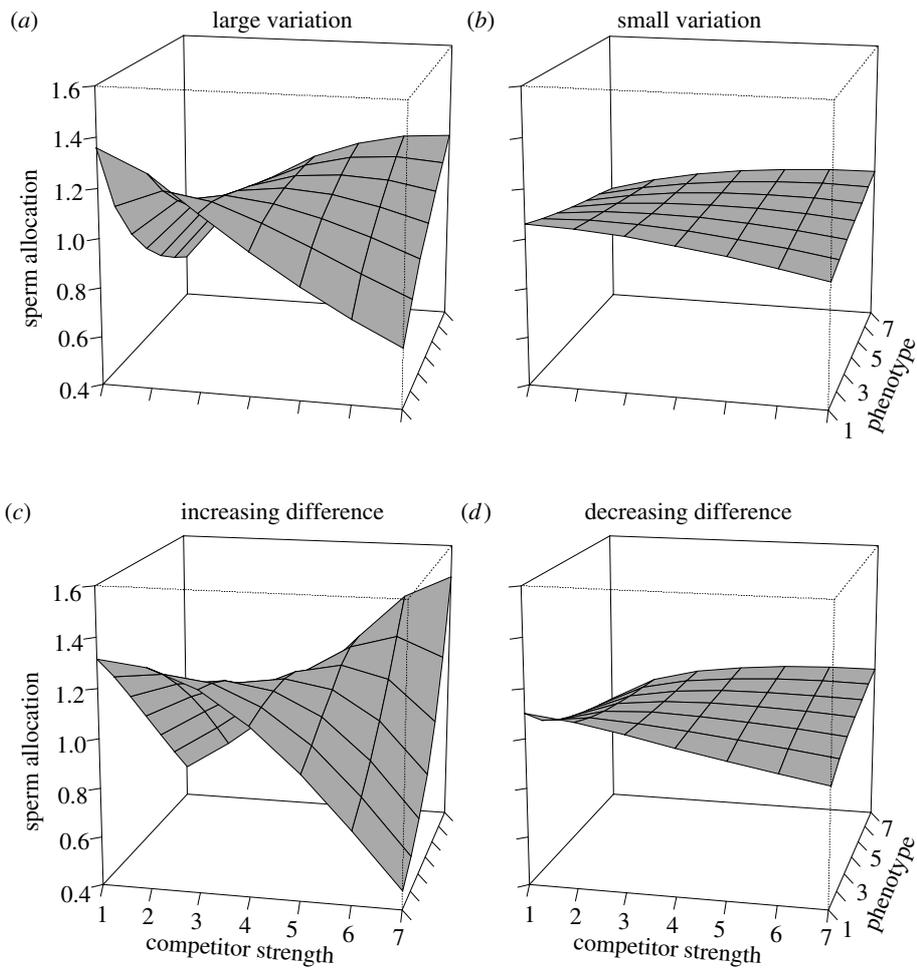


Figure 3. The ESS matrix S^* describing optimal sperm allocation for different male phenotypes in response to the sperm competition strength of competitors. Axes denotation is as in figure 2. In these simulations, uniform frequency distributions of male phenotypes (cf. figure 1a) were assumed.

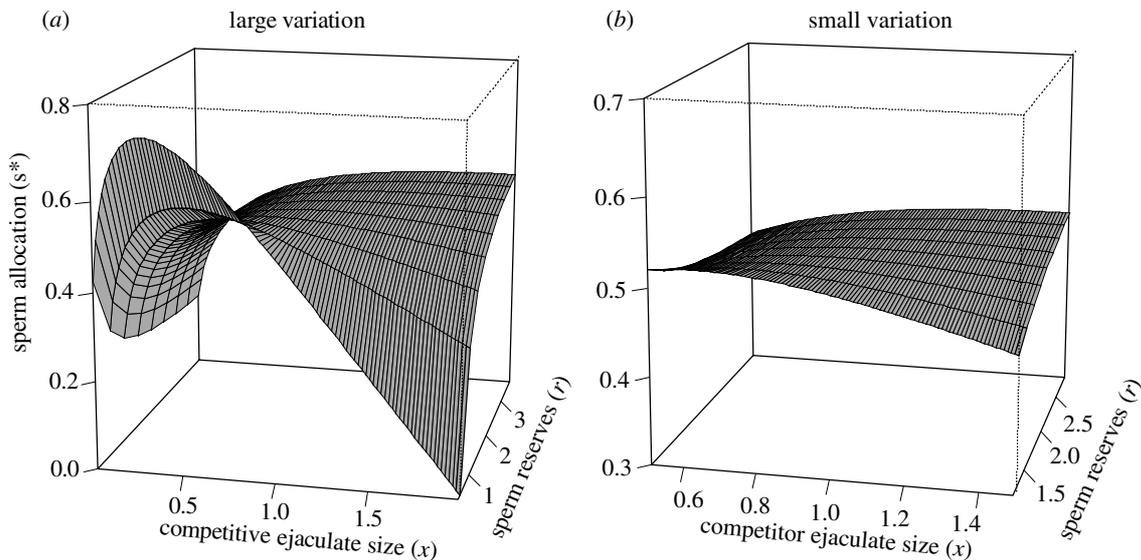


Figure 4. Curves describing optimal sperm allocation for males with sperm reserves equalling r in competition with an ejaculate of size x ; thus, the solution matrix maximizing $W(s, x) = s/(s + x) + \sum_{i=X_{\min}}^{X_{\max}} p_i(r - s)/((r - s) + X_i)$. In these calculations, a normal density probability function p_i for competing ejaculate size X was assumed. The average sizes of competing ejaculates were assumed to equal one unit of sperm. In (a), the solutions assuming large variances (s.d. = 0.2) in ejaculate size (X) are given, whereas in (b), relatively small variances (s.d. = 0.1) in X were assumed. Limits of the discrete integral equation X_{\min} and X_{\max} were set to $\bar{X} \pm 5$ s.d. and the number of intervals at 1000.

some of the important conclusions from the intensity model. The statement that males are predicted to expend most sperm in situations where they compete against an amount

of sperm equivalent to their own ejaculate size at mating seems to capture the essence of all three models, including the original intensity model (Parker *et al.* 1996).

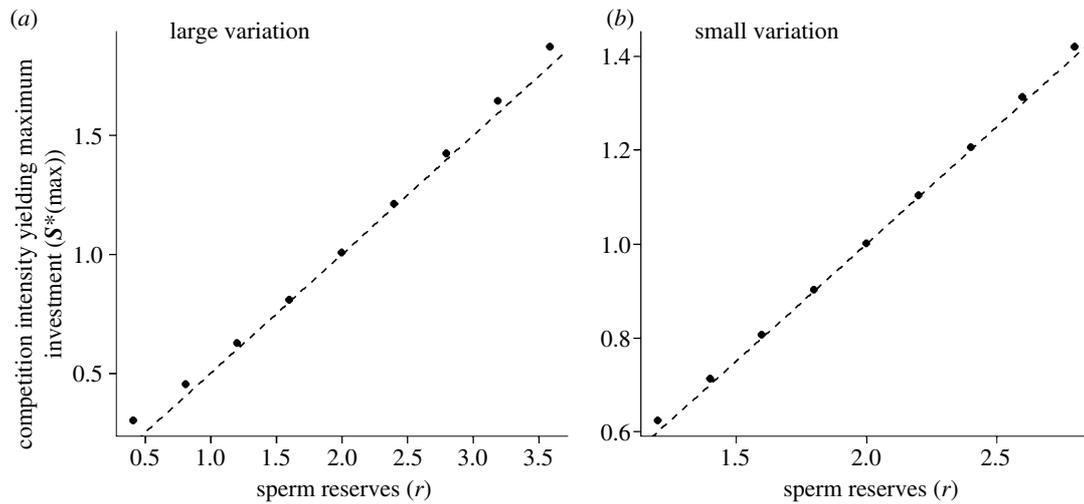


Figure 5. The predicted relation between the size of a male's sperm reserve (r) and the sperm competition intensity at which a male should expend the greatest amount of sperm. The dashed lines give the competition intensity equivalent to half of a male's sperm reserve ($y = r/2$). In (a), large variation (s.d./mean = 0.2) in competing sperm amounts was assumed, whereas in (b), small variation (s.d./mean = 0.1) was assumed (see also figure 4).

The accumulating evidence supporting the predictions from the sperm competition risk model (Parker 1990b; Parker *et al.* 1997) that males facing a high risk of sperm competition should expend more sperm is now overwhelming (see, e.g. review in Wedell *et al.* 2002). Evidence supporting the intensity model (Parker *et al.* 1996) is more scarce (Simmons & Kvarnemo 1997; Smith *et al.* 2003; delBarco-Trillo & Ferkin 2006) and not unambiguous (Gage & Barnard 1996; Fuller 1998; Schaus & Sakaluk 2001; Pilastro *et al.* 2002; Pizzarri *et al.* 2003; also discussed in Engqvist & Reinhold 2005). Naturally, not many studies have examined sperm allocation in response to differences in the size of competing ejaculates, as until now there have been no predictions for this situation. Yet, there are a few very interesting studies on butterflies, moths and fishes (Cook & Gage 1995; Wedell & Cook 1999a; Zbinden *et al.* 2004), which we think deserve a more elaborate discussion here.

In studies of the moth *Plodia interpunctella* and the butterfly *Pieris rapae*, there was a positive correlation between the male sperm allocation and the number of sperm stored previously by the female (Cook & Gage 1995; Wedell & Cook 1999a). The sperm precedence patterns in both of these species seem to follow a bimodal distribution with predominantly second male sperm precedence (Cook *et al.* 1997; Wedell & Cook 1998). Therefore, our theoretical conclusions are not completely applicable, as some of the assumptions are violated. However, in the light of the present analysis, these studies show some intriguing results. In these studies, variation in the number of sperm stored by females was achieved by mating them to males with different mating history. In the moth *P. interpunctella*, male successive matings seem to exploit male sperm reserves. Therefore, in matings with virgin females, spermatophores of virgin males contain the most sperm followed by once- and twice-mated males, respectively (see Cook & Gage 1995). Faced with these various levels of sperm competition, males expended most sperm in competition against ejaculates from virgin males, thus against the largest ejaculates. Interestingly, only virgin males were used as focal males. Thus, these results

fit our predictions well, as males with plenty of sperm reserves (virgins) expend an increasing amount of sperm with increasing size of competing ejaculates (cf. figure 4) and expend most sperm in competition against similar (virgin) males. In the study of the butterfly *P. rapae*, mated males increased sperm allocation in response to an increased number of sperm stored by females (Wedell & Cook 1999a). In *P. rapae*, virgin males transfer much less sperm in matings with virgin females than mated males do (Wedell & Cook 1999a,b). Thus, mated males spent more sperm in competition with mated males than in competition with virgin males. In their first mating, males seem to utilize only a small portion of their sperm reserves (Wedell & Cook 1999b). Therefore, it could be argued that mated males still have plenty of sperm reserves available compared with the low number of sperm stored by females mated to virgin males. Therefore, they should maximize allocation at a higher level of sperm competition intensity, which in fact they do (Wedell & Cook 1999a).

In sticklebacks (*Gasterosteus aculeatus*), males expend more sperm in matings if they perceive the presence of a large virtual competitor compared with matings in which the competitor was small (Zbinden *et al.* 2004). This was interpreted as evidence supporting the risk model of sperm competition (Parker *et al.* 1997), as larger males are probably better at stealing fertilizations through nest invasion (Zbinden *et al.* 2004). Alternatively, males may respond strategically to the sperm competition intensity. This would be in accordance with our analysis, provided that the fishes used in this study estimate the competition ability of large virtual competitors to be more similar to their own ability than small competitors.

In the present study, we have modelled the male's predicted response to variation in competing ejaculate size using two different approaches. In both the 'spawning' and the 'sperm storage' approaches, we reached similar and principally congruent conclusions. We hope that this study make it possible to evolve hypotheses and design sperm competition experiments for a wider range of situations and species than previously possible. Spawning species

where males often have a single competitor, which may differ in competitive ability, seem especially suitable for tests of our predictions.

REFERENCES

- Birkhead, T. R. & Møller, A. P. (eds) 1998 *Sperm competition and sexual selection*. San Diego, CA: Academic Press.
- 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., Harvey, I. F. & Parker, G. A. 1997 Predicting variation in sperm precedence. *Philos. Trans. R. Soc. B* **352**, 771–780. (doi:10.1098/rstb.1997.0061)
- Danielsson, I. 2001 Antagonistic pre- and post-copulatory sexual selection on male body size in a water strider (*Gerris lacustris*). *Proc. R. Soc. B* **268**, 77–81. (doi:10.1098/rspb.2000.1332)
- delBarco-Trillo, J. & Ferkin, M. H. 2006 Male meadow voles respond differently to risk and intensity of sperm competition. *Behav. Ecol.* **17**, 581–585. (doi:10.1093/beheco/ark001)
- Engqvist, L. & Reinhold, K. 2005 Pitfalls in experiments testing predictions from sperm competition theory. *J. Evol. Biol.* **18**, 116–123. (doi:10.1111/j.1420-9101.2004.00792.x)
- Engqvist, L. & Reinhold, K. 2006 Theoretical influence of female mating status and remating propensity on male sperm allocation patterns. *J. Evol. Biol.* **19**, 1448–1458. (doi:10.1111/j.1420-9101.2006.01134.x)
- Engqvist, L. & Sauer, K. P. 2001 Strategic male mating effort and cryptic male choice in a scorpionfly. *Proc. R. Soc. B* **268**, 729–735. (doi:10.1098/rspb.2000.1423)
- Engqvist, L. & Sauer, K. P. 2003 Determinants of sperm transfer in the scorpionfly *Panorpa cognata*: male variation, female condition and copulation duration. *J. Evol. Biol.* **16**, 1196–1204. (doi:10.1046/j.1420-9101.2003.00613.x)
- Fuller, R. C. 1998 Sperm competition affects male behaviour and sperm output in the rainbow darter. *Proc. R. Soc. B* **265**, 2365–2371. (doi:10.1098/rspb.1998.0585)
- 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. (doi:10.1007/s002650050251)
- Gross, M. R. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**, 263.
- Holland, J. H. 1975 *Adaptation in natural and artificial systems*. Ann Arbor, MI: University of Michigan Press.
- Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.
- Mitchell, M. & Taylor, C. E. 1999 Evolutionary computation: an overview. *Ann. Rev. Ecol. Syst.* **30**, 593–616. (doi:10.1146/annurev.ecolsys.30.1.593)
- Nakatsuru, K. & Kramer, D. L. 1982 Is sperm cheap? Limited male fertility and female choice in the Lemon tetra (Pisces, Characidae). *Science* **216**, 753–755.
- Olsson, M., Madsen, T. & Shine, R. 1997 Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proc. R. Soc. B* **264**, 455–459. (doi:10.1098/rspb.1997.0065)
- Parker, G. A. 1970 Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* **45**, 525–567.
- Parker, G. A. 1990a Sperm competition games: raffles and roles. *Proc. R. Soc. B* **242**, 120–126.
- Parker, G. A. 1990b Sperm competition games: sneaks and extra-pair copulations. *Proc. R. Soc. B* **242**, 127–133.
- 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), pp. 3–54. San Diego, CA: Academic Press.
- Parker, G. A., Ball, M. A., Stockley, P. & Gage, M. J. G. 1996 Sperm competition games: individual assessment of sperm competition intensity by group spawners. *Proc. R. Soc. B* **263**, 1291–1297.
- Parker, G. A., Ball, M. A., Stockley, P. & Gage, M. J. G. 1997 Sperm competition games: a prospective analysis of risk assessment. *Proc. R. Soc. B* **264**, 1793–1802. (doi:10.1098/rspb.1997.0249)
- Pilastro, A., Scaggiante, M. & Rasotto, M. B. 2002 Individual adjustment of sperm expenditure accords with sperm competition theory. *Proc. Natl Acad. Sci. USA* **99**, 9913–9915. (doi:10.1073/pnas.152133499)
- Pitnick, S. & Markow, T. A. 1994a Large-male advantages associated with costs of sperm production in *Drosophila hydei*, a species with giant sperm. *Proc. Natl Acad. Sci. USA* **91**, 9277–9281. (doi:10.1073/pnas.91.20.9277)
- Pitnick, S. & Markow, T. A. 1994b Male gametic strategies: sperm size, testes size, and the allocation of ejaculate among successive mates by the sperm-limited fly *Drosophila pachea* and its relatives. *Am. Nat.* **143**, 785–819. (doi:10.1086/285633)
- Pizzari, T. K. C. C., Løvlie, H., Jakobsson, S. & Birkhead, T. B. 2003 Sophisticated sperm allocation in male fowl. *Nature* **426**, 70–74. (doi:10.1038/nature02004)
- Reinhold, K., Kurtz, J. & Engqvist, L. 2002 Cryptic male choice: sperm allocation strategies when female quality varies. *J. Evol. Biol.* **15**, 201–209. (doi:10.1046/j.1420-9101.2002.00390.x)
- Schau, J. M. & Sakaluk, S. K. 2001 Ejaculate expenditures of male crickets in response to varying risk and intensity of sperm competition: not all species play games. *Behav. Ecol.* **12**, 740–745. (doi:10.1093/beheco/12.6.740)
- Schau, J. M. & Sakaluk, S. K. 2002 Repeatability of sperm number across multiple matings in three cricket species, *Grylodes sigillatus*, *Gryllus veletis*, and *Gryllus texensis* (Orthoptera: Gryllidae). *Can. J. Zool.* **80**, 582–585. (doi:10.1139/z02-012)
- Simmons, L. W. 2001 *Sperm competition and its evolutionary consequences in the insects*. Princeton, NJ: Princeton University Press.
- Simmons, L. W. & Kværnemo, C. 1997 Ejaculate expenditure by male bushcrickets decreases with sperm competition intensity. *Proc. R. Soc. B* **264**, 1203–1208. (doi:10.1098/rspb.1997.0166)
- Smith, C., Reichard, M. & Jurajda, P. 2003 Assessment of sperm competition by European bitterling, *Rhodeus sericeus*. *Behav. Ecol. Sociobiol.* **53**, 206–213. (doi:10.1007/s00265-002-0576-x)
- Stockley, P. & Seal, N. J. 2001 Plasticity in reproductive effort of male dung flies (*Scatophaga stercoraria*) as a response to larval density. *Funct. Ecol.* **15**, 96–102. (doi:10.1046/j.1365-2435.2001.00496.x)
- Sumida, B. H., Houston, A. I., McNamara, J. M. & Hamilton, W. D. 1990 Genetic algorithms and evolution. *J. Theor. Biol.* **147**, 59–84. (doi:10.1016/S0022-5193(05)80252-8)
- Warner, R. R., Shapiro, D. Y., Marcanato, A. & Petersen, C. W. 1995 Sexual conflict—males with highest mating success convey the lowest fertilization benefits to females. *Proc. R. Soc. B* **262**, 135–139.
- Wedell, N. & Cook, P. A. 1998 Determinants of paternity in a butterfly. *Proc. R. Soc. B* **265**, 625–630. (doi:10.1098/rspb.1998.0340)
- Wedell, N. & Cook, P. A. 1999a Butterflies tailor their ejaculate in response to sperm competition risk and intensity. *Proc. R. Soc. B* **266**, 1033–1039. (doi:10.1098/rspb.1999.0740)

- Wedell, N. & Cook, P. A. 1999b Strategic sperm allocation in the Small white butterfly *Pieris rapae* (Lepidoptera: Pieridae). *Funct. Ecol.* **13**, 85–93. (doi:10.1046/j.1365-2435.1999.00286.x)
- Wedell, N., Gage, M. J. G. & Parker, G. A. 2002 Sperm competition, male prudence and sperm-limited females. *Trends Ecol. Evol.* **17**, 313–320. (doi:10.1016/S0169-5347(02)02533-8)
- Zbinden, M., Largiadèr, C. R. & Bakker, T. C. M. 2004 Body size of virtual rivals affects ejaculate size in sticklebacks. *Behav. Ecol.* **15**, 137–140. (doi:10.1093/beheco/arg110)