Cryptic male choice: sperm allocation strategies when female quality varies

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Keywords:

cryptic mate choice;
evolutionary stable strategy;
genetic algorithm;
sexual selection;
sperm competition.

Abstract

We examined evolutionary stable sperm allocation and included stochastic variation in male mating frequency, not included in previous models examining sperm allocation strategies. We assumed sperm mixing and variation in female quality and used a genetic algorithm to analyse the evolution of male sperm allocation. Our results show that males should invest more sperm in initial copulations than in subsequent copulations as a male might fail to mate again. The inclusion of variation in female fecundity had no influence on the evolutionary stable sperm allocation strategy if males were unable to recognize female quality. If males were assumed to allocate sperm in response to female quality, the proportion of sperm allocated was positively correlated with female quality. Moreover, with increasing variance in female quality, males conserved more sperm for later copulations. Literature data on sperm allocation from diverse taxa show a good fit with the predictions given by our model.

Introduction

When females mate with several males and sperm mixing occurs, sperm competition will select for an increased amount of sperm transferred (Parker, 1982; Parker *et al.*, 1996, 1997). As a result, male ejaculates usually contain far more sperm than needed for the fertilization of all eggs. As first argued by Dewsbury (1982), single sperm may be cheap, but as males transfer large numbers of sperm, their ejaculate volume can nevertheless be limited (Squires *et al.*, 1979; Svärd & Wiklund, 1986; Pitnick & Markow, 1994; Cook & Gage, 1995; Savalli & Fox, 1999).

Usually males court females, whereas females often choose their mating partners among the available males (Andersson, 1994). Female choice need not be limited to whether she mates or refuses to copulate, and females might also bias reproduction among the males she mates with (Eberhard, 1996). Such female behaviour that may for example include facilitation of sperm displacement, prevention of sperm transfer to the spermatheca or preferential sperm use, has been termed cryptic female choice (Thornhill, 1983; Eberhard, 1996). The term cryptic indicates that such a choice is difficult to observe as it is not mating *per se* that determines male mating success. In analogy, we define cryptic male choice as any male behaviour that allows males to bias their investment in matings towards certain females (Bonduriansky, 2001; Engqvist & Sauer, 2001). Most species have a male biased operational sex ratio (OSR) and males can thus be expected not to choose overtly among females. But when sperm or any other investment in matings limits male reproductive success, males can be expected to choose cryptically by varying their investment when it pays them to do so (e.g. Simmons *et al.*, 1993; Gage & Barnard, 1996; Simmons & Kvarnemo, 1997; Gage, 1998; Wedell & Cook, 1999; Engqvist & Sauer, 2001).

The aim of the present theoretical study was to examine how female quality (i.e. fecundity) and the stochastic nature of male mating success will influence the optimal sperm allocation strategy. Many authors have examined how males should allocate their available resources, assuming that sperm production or transfer are costly to males (e.g. Parker, 1990; Parker *et al.*, 1996,

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1997; Fryer *et al.*, 1998; Galvani & Johnstone, 1998). The game theoretical modelling by Parker and coworkers (e.g. Parker *et al.*, 1996, 1997) has shown that males should invest less sperm in copulations with low sperm-competition risk (i.e. low probability of female polyandry) and high sperm competition intensity (i.e. high number of competing sperm). These models, however, did not address the influence of female fecundity variation and stochastic male mating success. Stochastic male mating success was included in the model by Fryer *et al.* (1998). For mathematical tractability, this model assumed males to mate with a maximum of two females. Under these assumptions males should at least allocate half of their sperm to their first copulation (i.e. invest more in the present copulation than is conserved for the uncertain future copulation). In a theoretical analysis using dynamic programming, Galvani & Johnstone (1998) examined the optimal sperm allocation strategy in a male life history perspective when female quality varies. Their simulations assumed a fixed male mating number, meaning that all males were assumed to mate ten times, males were therefore predicted to save most of the available sperm for future copulations. The obvious contrast to the results obtained by Fryer *et al.* (1998) is probably because of the assumption of a fixed number of mates a male will encounter, an assumption that will often be violated in nature, where males usually differ widely in mating frequency and where each copulation can be a male's last one. Moreover, Galvani & Johnstone (1998) concluded that under some conditions, especially under a sigmoid pay-off function, males should invest more sperm in copulations with medium quality females than in copulations with high or low quality females. Intuitively, males should invest more sperm in copulations with high quality females simply because the pay-off from these copulations should be higher. This will, on the other hand, increase sperm competition intensity in high quality females, which will tend to decrease optimal sperm allocation to high quality females (cf. Parker *et al.*, 1996). Therefore, the pattern of sperm competition, and hence the pay-off function of male investment will depend on the strategies of other males in the population. To elucidate the optimal sperm allocation strategy, fixed pay-off functions that are independent of male strategy frequencies as used by Galvani & Johnstone (1998) are inadequate. An approach using frequency dependent pay-offs, like game theory modelling (Maynard Smith, 1982) to determine the evolutionary stable sperm allocation strategy, is called for.

We addressed limitations of previous sperm allocation models, using a genetic algorithm to estimate the evolutionary stable sperm allocation strategy. This method mimics some aspects of natural selection and is based on game theory modelling. It includes competition of various strategies, considers the effect of competitors on reproductive success and for many problems allows detection of superior strategies close to the evolutionary stable strategy. For these simulations we assumed sperm mixing, a limited ejaculate volume and a stochastic male mating frequency. We examined how males should allocate their sperm over successive copulations in four simulation series that differed, (1) in the assumed variation in female quality (= fecundity), (2) in male ability to recognize this variation and (3) in male refilling of sperm stores. Table 1 gives a list of the combinations of these assumptions we have chosen in the four simulation series.

Material and methods

We used a genetic algorithm to estimate the evolutionary stable sperm allocation strategy of males when females mate multiply and when sperm mixing occurs. Genetic algorithms are a class of optimization tools, which are based on genetic systems and natural evolution (Holland, 1975; Toquenaga & Wade, 1996). Especially when the range of possible solutions is enormous, genetic algorithms are regarded as very effective search techniques (Sumida *et al.*, 1990). In our case, it is important that genetic algorithms can also be used to find solutions to game theory problems. In the genetic algorithm we used, females were assumed to mate randomly with the available males and each male was assigned a sperm allocation strategy that determined how the available sperm was allocated among his successive copulations. The success of each individual male strategy was evaluated by his reproductive success. As we assume sperm mixing, male reproductive success is estimated to be proportional to a male's share among the sperm a female has received. As a measure of male reproductive success we calculated the product of his share and female quality (i.e. fecundity) summed over all copulations of the male under consideration (eqn 1).

$$\textit{male reproductive success} = \sum_{C=1}^{C=n} Q_F \frac{S_C}{\sum S_F}$$

where C is the male copulation number, Q_F the female quality, S_c the sperm transferred in copulation c and $\sum S_\mathrm{F}$ the total sperm received by female during mating period.

Table 1 Description of conditions assumed in the four simulation series used to examine the evolutionary stable sperm allocation strategies. Within each simulation series, five independent repeated runs were conducted for each set of assumed parameters. Each simulation started with 100 random sperm allocation strategies, comprised 1000 populations per generation and a total of 500 generations.

Simulation series	Variation in female quality	Males can detect female quality	Sperm refilling
I	–	–	–
II	+	–	–
III	+	+	–
IV	+	+	+

As in other simulations using genetic algorithms, only those males with a reproductive success among the top 50% were assumed to contribute to the next generation. This procedure helps to maintain genetic variation under strong selection and is a standard selection procedure used in genetic algorithms (Forrest, 1993). Between successive generations, mutation and crossover were assumed to occur. Within each simulation series, simulations were independently repeated for five runs with each set of assumed parameters. The results received in these repeated runs converged after several hundred generations and throughout the manuscript we report the strategies received after 500 generations.

The basic model

We assumed discrete generations that consisted of populations of 100 males and 100 females. Males were assumed to produce sperm only prior to the mating period. In each population, copulations were assumed to take place within a period of 10 days and prior to the production of any offspring. We assumed diverse female mating frequencies (i.e. number of matings per female), leading to various OSR. For low OSR, many males have no chance to reproduce on a given day. Because of this stochastic uncertainty and because of the limited mating period, any copulation could be a male's last one. Within each simulation, all females where assumed to have the same number of mates (from two to ten). For each individual female the days the female was assumed to be receptive were randomly assigned. Within each day, males were randomly assigned among receptive females so that each receptive female mated with one male (e.g. a female with mating frequency of three might be assigned to mate on days 2, 5 and 7 of the 10 day mating period). Each male also had a maximum mating frequency of one mating per day.

In all simulations, 100 random sperm allocation strategies were generated at the beginning of the first generation. Such a sperm allocation strategy comprises ten values that determine the proportion of the available sperm that is transferred during a copulation. The first value gives the proportion of available sperm that is transferred during the first copulation, the subsequent values give the proportion of the remaining sperm that is transferred during the male's second to tenth copulation. Assuming random sperm mixing and an identical initial sperm supply of all males, the reproductive success of each male was calculated as being proportional to his share among the sperm of the females the male mated with. To receive reliable estimates for the reproductive success of male genotypes, the described simulation was repeated for the same male types in 1000 populations. Within each generation, the 50 sperm allocation strategies with the highest average reproductive success in these 1000 populations were used to generate the sperm allocation strategies of the next generation. With the help of this procedure, which simulates the average success of 1000 males having the same genotype with regard to their sperm allocation strategy, we were able to select those strategies that were superior as a result of their sperm allocation pattern and not because of more frequent mating. Each of the selected 50 sperm allocation strategies was used twice so that 100 offspring could be generated. For each of those 100 cases, crossover was simulated and a crossover partner was randomly selected among the top 50 males. Subsequently, the ten values for the offspring sperm allocation strategy (for allocation to each mating) were randomly chosen from the given two strategies. After this process, we randomly selected 10% of the 1000 values given as the sperm allocation strategy of the 100 offspring males and changed them by adding a randomly selected value between –0.1 and 0.1. If this process, which was included to simulate mutation, led to negative values, the respective sperm allocation value was altered to zero. Likewise, sperm allocation values were altered to one when values above one occurred.

The described process led to a quick convergence towards a local maximum in reproductive success in all simulations. Although for each set of parameters the five repeated simulations started with different sets of strategies, all repeated simulations resulted in very similar sperm allocation strategies (see Fig. 1) and the achieved local maximum thus probably is the global maximum. Here, one should note that sperm allocation strategies are close to neutral when most sperm have been spent in previous copulations (Fig. 1). From the

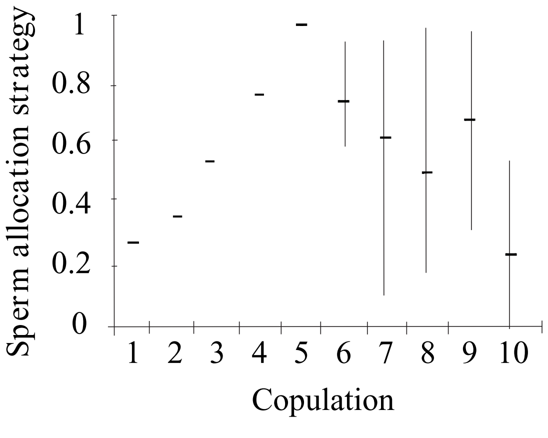

Fig. 1 Received sperm allocation strategies (relative proportion of available sperm invested per copulation) from five independent simulations (mean given as horizontal and range given as vertical bar) assuming that females mate five times. The bar at copulation number three indicates that males are predicted to spend about 50% of the sperm that is left after copulation number two when mating a third time. The large variation concerning sperm allocation strategies in copulations 6–10 results because almost all of the remaining sperm are spent during copulation number five; selection is therefore nearly absent for later copulations and the strategies are accordingly mainly influenced by drift.

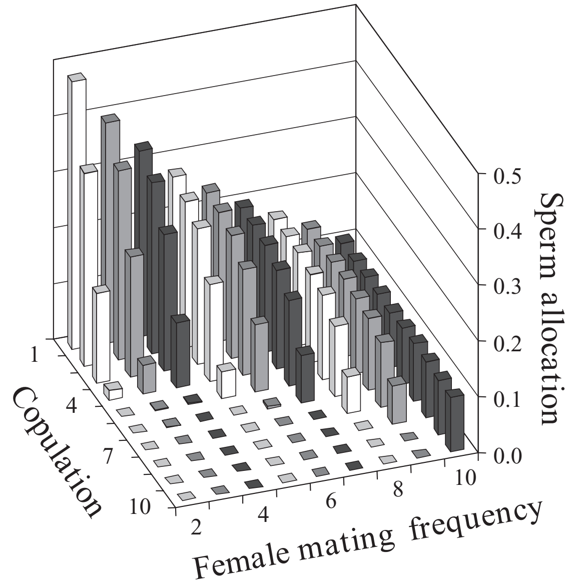

Fig. 2 Evolutionary stable sperm allocation (absolute proportions of sperm) for various female mating frequencies if variation in female quality is absent. For each female mating frequency, five independently repeated simulations were conducted. The bars give the mean values from these five independent simulations for the relative sperm investment in the first, second and up to the tenth copulation of a male; the variation between simulations was small ($CV = 0.028$).

sperm allocation strategy values, which give the proportion of the remaining sperm that is spent in the present copulation, we calculated the absolute proportion of sperm that is spent in each copulation. These absolute proportions are reported in Figs 2–5. The SD for the proportion of sperm invested in one copulation was smaller than 0.02 between the five repeated simulations in all cases shown in Figs 2 and 3. For those 59 values indicating that males should invest above 5% of their sperm, the average coefficient of variation (CV) (SD divided by the mean) calculated for the repeated simulations was 0.028.

Modelling variation in female quality

In the first simulation series, the described genetic algorithm was used to estimate the evolutionary stable sperm allocation strategy for different female mating frequencies when females were assumed to have equal fecundity. In a second and third series of simulations we estimated the evolutionary stable sperm allocation strategy when female quality (i.e. female fecundity) varies. In the second series of simulations we assumed that males were unable to recognize female quality and in the third series we assumed that males can adjust their sperm allocation in accordance with female quality. In these two simulation series, five classes of female quality were assumed. In the third series, male sperm allocation strategy was accordingly given by a 10 × 5 matrix. Each value in this matrix gives the proportion of the available sperm that is spent during the first, second, and up to the tenth copulation given that female quality is of class 1, 2, 3, 4 or 5. Female quality was assumed to vary in a multiplicative fashion, so that fertility differed by a certain factor between adjacent female quality classes and female quality is given relative to median quality females. We varied the assumed factor determining variation in female quality to examine the influence of female quality variation on the evolutionary stable sperm allocation strategies.

With variation in female quality, the type of females a male mates with has a large effect on his reproductive success. Therefore, the top 50% of the males may thus mainly be those that by chance mated often with high quality females. To prevent this effect from masking differences in male reproductive success that are because of male sperm allocation strategies, we used a round robin system. In the first population, females were modelled to mate randomly with the available males. In the second population, male 1 was assumed to have the same mating success – regarding the number, quality and sequence of types of females – as male 2 had in the first population; male 2 was assumed to have the mating success of male 3 in the first population and so on until male 100 that was assumed to have the mating success of male 1 in the first population. This process was repeated so that in the resulting 100 populations, average female quality was the same for all males. A male's reproductive success thus mainly represents how good his sperm allocation strategy is compared with the strategies of the other males. For each generation the described process was repeated ten times and 1000 populations were thus modelled per generation as in the other simulation series. To demonstrate that the used round robin system does not change the evolutionary stable sperm allocation strategy we compared the outcome of the round robin system with some selected simulations without this system using 10 000 populations and 10 000 generations. The round robin system led to very similar results but enabled a much quicker convergence to the evolutionary stable sperm allocation strategy. And, it probably gives more reliable estimates because it resulted in a lower variation between the five repeated runs.

Assuming sperm replenishment

In all the previously described simulations, males produced sperm only prior to the reproductive period. To examine whether sperm replenishment alters the evolutionary stable sperm allocation strategy, additional simulations (series IV) assumed that males were able to produce 10% of a full sperm complement per day after they spent sperm in a mating. Here, we assumed that

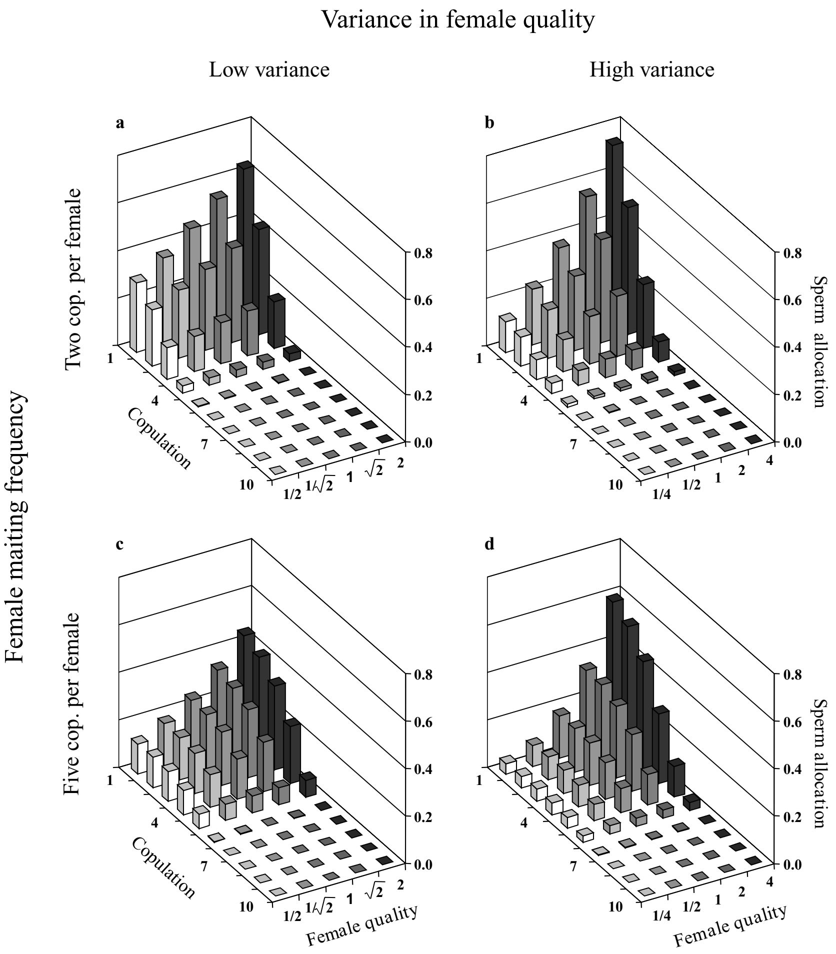

Fig. 3 Influence of female quality on the evolutionary stable absolute sperm allocation for two different female mating frequencies (two and five copulations per female; see top and bottom panels), and for a different amount of variation in female quality (the five classes of females are assumed to differ by a factor of √2 and 2, respectively; see left and right panels) given males can recognize variation in female quality. Here, each graph gives the average sperm allocation values from five independently repeated simulations.

sperm production stops when the initial sperm number is reached (i.e. when the sperm reservoir is filled again).

Results

With a low female mating frequency, males should transfer most of their sperm during the first few copulations. When females are assumed to mate as often as males are able to mate (i.e. when the OSR approaches one), males can be expected to invest their sperm more evenly among subsequent copulations. The sperm allocation strategies that resulted from our simulations are in accordance with these expectations (Fig. 2). With an OSR of one, males spend their sperm evenly among females. For all OSRs below one, i.e. for female copulation frequency below 10, copulations without sperm transfer occurred, because males had invested all their sperm in preceding copulations.

If female quality was assumed to vary but males being unable to detect female quality, the resulting sperm allocation strategy was very similar to the case with no variation in female quality. For an assumed quality variation between 0.25 and 4 times the quality of median females and when females were assumed to mate two times, males are expected to transfer on average 48.5, 34.3, 15.6 and 1.5% of their sperm during the first four copulations. A comparison of these values with the results of the simulations that assumed no variation in female quality (Fig. 2) shows very similar values (47.8, 34.5, 16.0 and 1.6%). Considering the mean sperm allocation strategies for the first four copulations, there was an absolute difference between models of only 0.35%. Moreover, there was no significant difference between models when the sperm allocation strategies of the first four copulations (differences are unlikely for later copulations) of all ten simulations were compared [two-factorial ANOVA, two models (= treatments) and received sperm allocation strategies for the first four copulations as the two factors and five repeated simulations for each of those eight cases; $F_{1,32} = 0.01$, $P > 0.9$].

When female quality was assumed to vary and when males were assumed to recognize variation in female quality, male sperm allocation changed with female quality (Fig. 3). Males invested a larger proportion of

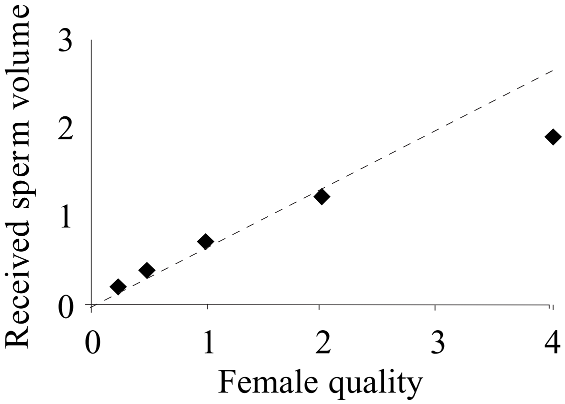

Fig. 4 Average sperm allocation (relative to initial sperm volume of a male) with regard to female quality when females are assumed to mate five times. The hatched line indicates the theoretical values that would result if the sperm per egg ratio would be independent of female quality, i.e. under an ideal free distribution of sperm among females. As high quality females receive fewer sperm and low quality females more sperm than indicated by this line, the success per sperm volume is higher in high quality females than in low quality females.

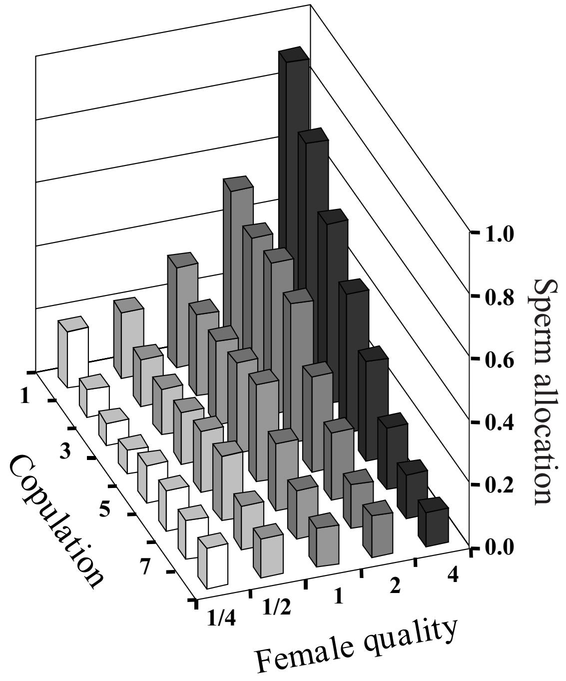

Fig. 5 Evolutionary stable sperm allocation (absolute proportions of sperm) assuming that males can replenish 10% of their sperm between days. Here, female remating frequency of 5 and high variation in female quality were assumed. The bars give the mean value for the relative sperm investment in the first, second and up to the tenth copulation of a male that we received in five independent simulations.

their available sperm when mating with high quality females. This difference was especially obvious during initial copulations and diminished later during subsequent copulations. Consequently, high quality females received, on average, more sperm than females of lower quality (Figs 3 and 4). However, high quality females having four times the fecundity of median females did not receive four times as many sperm as median quality females. And, low quality females having 0.25 times the fecundity of median females received more than one-fourth the sperm volume median quality females received. Therefore, the egg to sperm ratio remains positively correlated with female quality and the gain per invested proportion of sperm is thus still positively correlated with female quality. This can be seen in Fig. 4 by comparing the received sperm amount – given as diamonds – with the expectation that females receive sperm in accordance with their fecundity. The expected values were calculated under the assumption of an ideal free distribution (Fretwell & Lucas, 1970) of sperm among females and are given as a line in Fig. 4. Our results show that high quality females receive fewer sperm per egg than the other females meaning that gain in reproductive success per invested sperm amount is still highest in high quality females.

Increasing the magnitude of female variance led to a modest increase in the average investment in late copulations (compare left and right parts of Fig. 3). Under low variance in female quality, males spent on average 0.2% of their sperm in the sixth copulation, and 3.2% under high variance in female quality.

If males were assumed to be able to refill their sperm reservoirs during the mating season, the resulting sperm allocation strategies indicate that males should invest a larger proportion of the available sperm in initial matings than they should without the opportunity to produce new sperm (Fig. 5). However, male ability to refill sperm stores did not change the pattern of the resulting evolutionary stable sperm allocation strategy: sperm investment in copulations increased with female quality but in a way that gains per investment were still larger in females of higher quality. In addition, males still invest more sperm in initial copulations than in subsequent copulations (Fig. 5).

Discussion

Our simulations predict that males should invest more sperm in the first copulation than in subsequent copulations and more sperm in high quality females than in low quality females. However, males can be expected to vary sperm investment less than the existing variation in female quality. With high variance in female quality, males should modestly decrease their investment in early copulations compared with situations of low variance in female quality. The general pattern of the received evolutionary stable sperm allocation strategies did not change when males were assumed to replenish their sperm supplies.

Based on our simulations we propose that males should invest more sperm in initial copulations because each copulation can be a male's last one. Only when we assumed an OSR of one, evolutionary stable sperm allocation strategies comprised an even distribution of sperm between copulations, although this result should only hold if there is zero reproductive skew. In their mathematical treatment of a similar problem Fryer *et al.* (1998) came to the same conclusion that males usually spend more sperm in initial copulations. Their model assumed a maximum mating frequency of two for males and females. The present study extends these conclusions and shows that they are also valid for male and female remating frequencies of more than two. If a male invests all of its sperm in its current mate, the reproductive success gained by the last sperm transferred might be lower than if these sperm are saved and transferred in the next copulation. This disadvantage that stems from numerical competition among self-sperm is counterbalanced by the chance that a male will not mate again. As males transfer only few sperm during later copulations – they already have spent most of their sperm during previous copulations – the effect of numerical competition within a male's ejaculate decreases. At a certain point, males benefit to spend most or all of their sperm during the present copulation because the advantage of saving sperm is less important than the disadvantage from the risk of achieving no further fertilizations. Two additional mechanisms not considered in this model could further select for an increased sperm expenditure in initial matings. First, females might respond with an increased remating rate to copulations where they receive small ejaculates. Such a behaviour also selects for an increased sperm allocation in initial copulations because it will not pay males to save a small proportion of their sperm for future copulations. Secondly, another possible factor that may also devalue male future reproductive success – male mortality – was not incorporated in our simulation. If male mortality occurs during the mating period, males should invest even more sperm in initial copulations.

The experimental data on sperm allocation we could find in the literature fit the predictions of our simulations well. In species where female remating frequency is low, males invest more sperm in the first copulation than in further copulations (Squires *et al.*, 1979; Svärd & Wiklund, 1986; Pitnick & Markow, 1994; Cook & Gage, 1995; Savalli & Fox, 1999). In several species of voles, males seem to invest about 50% of the available sperm in an initial copulation and about 30% of the available sperm in a second copulation (Pierce *et al.*, 1990). In *Drosophila acanthoptera*, a species with about 50% of the females mating twice, provisioning experimental males with several receptive females within a short period of time, led to the following proportions of sperm transferred during the first three copulations: 50, 34 and 16% (Pitnick & Markow, 1994). The empirical values from voles and fruit flies correspond closely with the theoretical ones given in Fig. 2, where females were assumed to mate twice: 48, 35 and 16%. Moreover, in closely related *Drosophila* species with frequent remating in females, males spend only a small proportion of the available sperm (Pitnick & Markow, 1994) in accordance with the predictions of our model (see Fig. 2, high female mating frequency).

Our simulations predict that males should allocate more sperm to high quality females. As a result, high quality females received more sperm than low quality females. Using the ratio between female quality and received sperm volume, one can compare the gain from copulations with high quality and low quality females. Although high quality females received more sperm than low quality females, the gain per sperm volume was still larger for high quality females (Fig. 4). This deviation from an ideal free distribution is related to the stochastic nature of male mating success. Males do not necessarily mate with a set of females balanced for their quality and they might thus only have restricted opportunities for choice. In addition, uncertainty of future copulations will select for an increased sperm investment in low quality females in comparison with an ideal free distribution.

According to our simulations, males can be expected to invest more sperm when mating with high quality females. In this sense, our results are analogous to those received by Parker *et al.* (1996) concerning sperm competition intensity. In copulations with high quality females, males should increase investment as sperm competition intensity (number of competing sperm per egg) is low compared with matings with low quality females. Our results also coincide with experimental data. First, males of a coral reef fish and dung flies invest sperm correlated with the number of available eggs but less than proportional to egg number (Shapiro *et al.*, 1995; Parker *et al.*, 1999), as predicted by our model. In addition, several studies examining the effect of female quality on male investment show that males invest more in high quality females than in medium or low quality females (Gage & Barnard, 1996; Gage, 1998; Sauer *et al.*, 1998; Parker *et al.*, 1999; Wedell & Cook, 1999; Engqvist & Sauer, 2001). In contrast, Simmons & Kvarnemo (1997) found that male *Kawanaphila* bushcrickets invest less sperm in matings with larger and eventually more fecund females. But in this species, larger females mate more often than small males so that sperm competition per egg probably becomes more intense in larger females. In each simulation of the present study, all females had the same mating frequency and the conclusions made are only valid as long as there is no correlation between female quality and mating frequency. The benefit of higher sperm allocation in copulations with high quality females will also influence the optimal sperm allocation in successive matings. On average, males will save more sperm to subsequent matings when the variance in female quality is high, because then, the selection on males to save sperm for future copulations with high quality females will be higher than with lower variance in female quality. However, the magnitude of this effect was weak. The simulations, where the best females were 16 times better than the lowest quality females, resulted in modest changes of the sperm allocation strategy compared with simulations with no variance in female quality.

In contradiction to our main results, Galvani & Johnstone (1998) concluded that males should invest more sperm in medium quality females than in high quality females and that males during initial copulations should save most sperm for later copulations. In their simulations, they assumed that sperm competition is most intense in high quality females and they accordingly received the result that males should prefer medium quality females. However, if medium quality females are preferred, sperm competition should be most intense in these. This contradiction between assumptions and conclusions of the model resulted because it did not include the effect of sperm allocation strategies on sperm competition intensity. Such frequency dependent effects are, in contrast, an integral part of game theory models and were incorporated in our model. The conclusion that males should save most sperm for later copulation likewise depends on unrealistic assumptions of the simulation of Galvani & Johnstone (1998). Under realistic conditions, males will usually not have similar mating success and males almost always run the risk of not finding another mate and thus wasting all sperm saved in an initial copulation. In contrast to the model of Galvani & Johnstone (1998), our simulations did include the effects of variation in male mating success by assuming stochastic variation.

In our simulations we modelled male sperm allocation strategies. The results of our model should, however, also be valid for other resources that are limited and have an influence on sperm competition and hence represent mating effort. In species where male sperm transfer depends on the size of nuptial gifts, for example, scorpionflies (Sauer *et al.*, 1998), crickets (Sakaluk, 1984, 1985), or bushcrickets (Reinhold & Heller, 1993), males can be expected to vary their investment in a similar way as with a limited sperm supply. Actually, male *Panorpa vulgaris* scorpionflies invest more saliva secretions in copulations with high quality females (Sauer *et al.*, 1998) and the increase in investment is less than proportional to the increase in female quality (K. P. Sauer, personal communication) as predicted by our model. Also, in accordance with our simulations, male effort for sperm transfer as well as nuptial gift size are positively correlated with female quality in *P. cognata*, another scorpionfly species, and males thus choose cryptically and transfer larger nuptial gifts and more sperm to females with high fecundity (Engqvist & Sauer, 2001; L. Engqvist & K. P. Sauer, unpublished data).

In conclusion, our simulations depict how males should invest a limited sperm supply in subsequent copulations when female quality varies. Empirical data from the literature on sperm allocation in subsequent copulations and on sperm investment if female quality varies show a close match to the predictions of our simulations.

Acknowledgments

We thank Amos Bouskila, Kirsten Klappert, Bernhard Misof, Klaus Reinhardt, Bernhard Roitberg and Gabriele Uhl for discussion and comments on previous versions of the manuscript.

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Received 12 November 2001; accepted 14 December 2001