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Minireview

Sperm dumping as a defense against meiotic drive

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Abstract

Sperm from *Drosophila simulans* that carry a sex-ratio distorter is preferentially lost from females' sperm-storage organs. This suggests that sperm dumping is a major factor affecting sperm competition in this species, and may have evolved in response to sex-ratio distorters.

Meiotic drivers are genes that subvert the normal rules of inheritance to ensure that they are present in more than their fair share of gametes in the next generation [1]. For example, the driver *sex-ratio* (SR) in the fruit fly *Drosophila simulans* is an X chromosome that is present in all the sperm produced by male carriers, thus causing SR males to produce only daughters (Figure 1). This is because sperm carrying the Y chromosome in these males fails to develop properly. Early genetic analyses suggested that these drivers should increase in frequency in the population, as male carriers pass the driver on to all their offspring [1,2]. The SR was also predicted to outcompete normal X chromosomes because of the increased number of offspring in the population receiving the driving X. Eventually, the driver should reach such a high frequency that the population would consist entirely of females - and would go extinct. In reality, drivers do not seem to spread to fixation. In wild populations, drivers are often found at a low but stable frequency, and in laboratory populations SR and other drivers are usually outcompeted by non-driving chromosomes [2]. Furthermore, experimental studies have shown that this failure to spread is probably caused by reduced competitive ability of driving males' sperm [3].

In males carrying SR, for example, the failure of the sperm that carry the Y chromosome could reduce the total amount of functioning sperm produced. This in turn might reduce the amount of sperm that the male transfers to a female. If a female mates with more than one male, the sperm will mix inside her and compete to fertilize her eggs, and the male transferring the most sperm is generally expected to fertilize the majority of eggs [4]. Male carriers of sex-distorter genes, whose sperm production is limited by the killing of non-driving sperm, may be poor sperm competitors as a result [5].

Previous work has indeed found that carriers of meiotic drivers are generally poor sperm competitors compared with non-carrying males [3], and this is assumed to be due to direct competition between sperm, with males that transfer more sperm being more successful. A recent paper by Angelard and co-workers [6], published in *BMC Evolutionary Biology*, now challenges this assumption, by showing that female response to sperm quantity may be more important than direct competition between the sperm.

Angelard and her colleagues investigated SR drive in *D. simulans*. They mated virgin females to either a male carrying

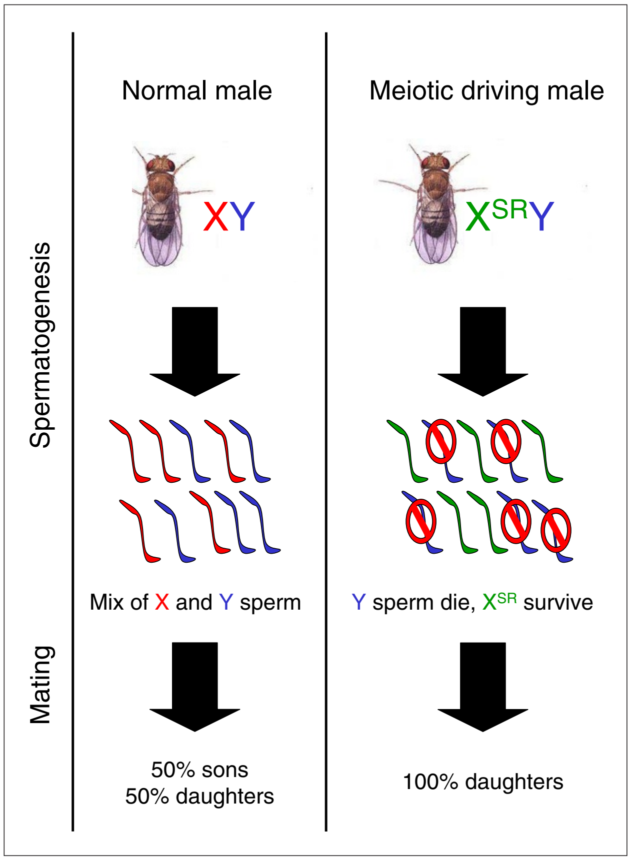

Figure 1
The *Sex-ratio* (SR) meiotic driver eliminates sperm carrying the Y chromosome, resulting in males that produce only daughters.

the SR driver or a normal male. They then removed and counted the sperm both in the uterus, indicating the amount transferred, and in the female's sperm-storage site, indicating the amount stored by the female for use in fertilizing eggs. Males that carried the SR driver were found to transfer half the number of sperm of normal males. After 24 hours, the proportion of a male's sperm in storage was the same, irrespective of male genotype. However, four days after mating, there was a significantly greater drop in the number of stored sperm from males carrying the SR driver (compared with that from normal males), suggesting that the 'driving' sperm was preferentially discarded by females. The authors confirmed that this effect was not simply due to a higher death rate of SR sperm in storage by assaying sperm mortality rate. Although SR sperm did show a higher mortality rate than normal sperm, the difference was not large enough to account for the observed decrease in sperm numbers.

The authors could not determine directly whether the removal of SR males' sperm was due to a specific response by females to sperm carrying the SR driver, or was simply a response to receiving small ejaculates. There is little previous evidence that females can detect meiotic drivers in sperm, and it therefore seems likely that *D. simulans* females were responding to the significantly smaller ejaculates transferred by SR males. This possibility could be tested in future studies by using multiply mated normal males, which transfer smaller ejaculates.

Angelard and co-workers also allowed females to remate with a second male, allowing either sperm transfer or interrupting the mating to allow seminal fluid but not sperm to be passed to the female. Seminal fluid contains a wide range of proteins that directly affect sperm competition and sperm survival [7]. Previous work, mostly on the closely related *D. melanogaster*, suggests that both sperm and accessory fluid have strong impacts on the sperm stored from the first mating [7]. In Angelard's study, however, the second mating did not affect the release of sperm from the first mating, whereas the genotype of the first male had a very strong impact [6].

It has been suggested that female responses to meiotic drivers may play an important role in preventing their spread through populations. For example, females could remate more often when there is a risk of mating with SR males, thereby promoting sperm competition that reduces the paternity of SR males [8]. Although sperm dumping has previously been suggested as a major factor affecting the outcome of sperm competition in *D. melanogaster* [9], this is the first time it has been proposed to directly regulate the spread of meiotic driving genes. Indeed, this work raises the possibility that the preferential dumping by females of sperm from small ejaculates might have evolved as a way to reduce the risk of driving males fathering offspring. There are other possible explanations, however. For example, sperm loss could be a by-product of selection for something else; conditions in the female sperm-storage organ are potentially damaging to sperm, and large ejaculates may be better able to buffer against female spermicide and hence survive longer. Certainly the uterus of a female *Drosophila* is a very unfriendly environment for sperm, possibly as a side effect of mechanisms for preventing infection taking hold in the vulnerable reproductive tract [10].

Angelard *et al.* [6] used strains of *D. simulans* that had been maintained in the laboratory for many generations, and throughout this time adult females and males were kept together. As a result, females were unlikely to ever run out of sperm. It would be interesting to examine whether differential loss of sperm also occurs in wild populations harboring meiotic drivers. In some populations, sperm may be a far more valuable resource for females, which might reduce their willingness to dump it. In particular, in populations that harbor a high frequency of SR or other sex-ratio distorters, males (and therefore sperm) may be in short supply. Under these conditions, would females still dump sperm from small ejaculates? And if they did not, would this increase the spread of the driver through the population? The work by Angelard *et al*. brings evidence of an important new mechanism to work on meiotic drive, and should stimulate further research in this area.

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