NEWS & COMMENT

How to gain the benefits of sexual reproduction without paying the cost: a worm shows the way

Sexual reproduction is perhaps the greatest of all evolutionary puzzles. It's a puzzle because sexually reproducing species pay the cost of spending half their resources (over and above what is needed for vegetative growth) in producing males, whereas parthenogenetic species utilize all their resources meant for reproduction in producing only females (or hermaphrodites) like themselves. This twofold cost of sexual reproduction[1,2] is sometimes referred to as the twofold cost of producing males. Three advantages of sexual reproduction that might offset this cost have been proposed. Genetic recombination and cross fertilization permit sexually reproducing species to (1) bring together, in the same individual, mutations arising in different individuals[3,4]; (2) generate genetic variability and thus adapt to changing environments[2,5,6]; and (3) shuffle their genes in every generation and thus keep parasites at bay[7–9]. While evolutionary biologists are busy testing their favourite ideas for offsetting the twofold cost of producing males, recent work by Craig LaMunyon and Samuel Ward[10] shows that a nematode, *Caenorhabditis briggsae*, appears to have found a way of gaining the benefits of sexual reproduction without paying the cost of producing males.

Before we understand how the worm accomplishes this, it would be useful to familiarize ourselves with its more famous cousin, *C. elegans* – a remarkable nematode that was chosen by geneticists after a deliberate search for a simple multicellular eukaryote[11,12]. It is 1 mm long and has <1000 cells in its body. Most individuals are hermaphrodites, which produce both oocytes and sperm and reproduce by self-fertilization. Males are occasionally produced because of nondisjunction of the X chromosomes. Hermaphrodites have two X chromosomes and hence their oocytes and sperm each carry a single X chromosome. Males carry a single copy of the X chromosome and are designated XO. Their sperm may either carry a single copy of X or may carry no copies – the latter are designated nullo-X. Occasionally, hermaphrodites mate with males and produce outcrossed male and hermaphrodite offspring. Perhaps because mating is so rare, the worm makes the best use of the opportunity available and produces nearly all outcrossed progeny. Both the X-bearing and nullo-X sperm of the male take precedence over the sperm of the hermaphrodite, so that roughly equal proportions of outcrossed male and outcrossed hermaphrodite offspring are produced. Thus, even *C. elegans* pays the twofold cost of producing males to gain the advantage of sexual reproduction (Fig. 1). However, given the advantage of outcrossing, it should be expected that both the male and the hermaphrodite cooperate to suppress the hermaphrodite sperm – the male can preferentially transmit his genes and the hermaphrodite gains the advantage of sexual reproduction.

LaMunyon and Ward[10] have compared *C. elegans* with *C. briggsae* and found that the latter adopts an even better strategy. During the early period after mating, *C. briggsae* hermaphrodites produce only ~10% male offspring instead of the expected 50%. The remaining 90% hermaphrodite offspring are nearly all outcrossed progeny (Fig. 1). This was revealed by a trick employed by the experimenters – although the males were wild type, the hermaphrodites used for mating were homozygous for a recessive mutation that produces short and fat worms, appropriately referred to as 'chubby'. Thus, hermaphrodite progeny resulting from self-fertilization would be 'chubby', but those resulting from outcrossing would be wild type. The observation that only about 10% of the offspring were male and the remaining 90% of offspring were all wild-type hermaphrodites suggests that the X-chromosome-bearing sperm of the males took precedence not only over the sperm of the hermaphrodite (as in *C. elegans*), but also over the nullo-X sperm of the males (unlike *C. elegans*). Therefore, when presented with an opportunity to mate and outcross, *C. briggsae* worms gain the benefits of sexual reproduction without paying the cost of producing males.

It is clear that this process concerns competition between sperm rather than the enhanced survival of outcrossed hermaphrodite offspring relative to outcrossed male offspring (mortality of progeny was found to be independent of their gender). It is also clear that sperm competition is not a result of numerical dominance – another unusual, but very useful, character of *Caenorhabditis* is their extreme economy of sperm production and use. The numbers are so small and their use is so efficient that LaMunyon and Ward were able to account for all the sperm and show that male sperm can outcompete hermaphrodite sperm even when they are outnumbered by two to one. Even during selfing, each sperm is used to fertilize one oocyte. In contrast to most other organisms, oocytes are made in excess and some of them can remain unfertilized. As they mature, the oocytes reach the entrance of the spermatheca, where the lumen opens to release sperm. The oocyte then appears to 'ingest' a single sperm (fertilization) and excess sperm get swept into the uterus but
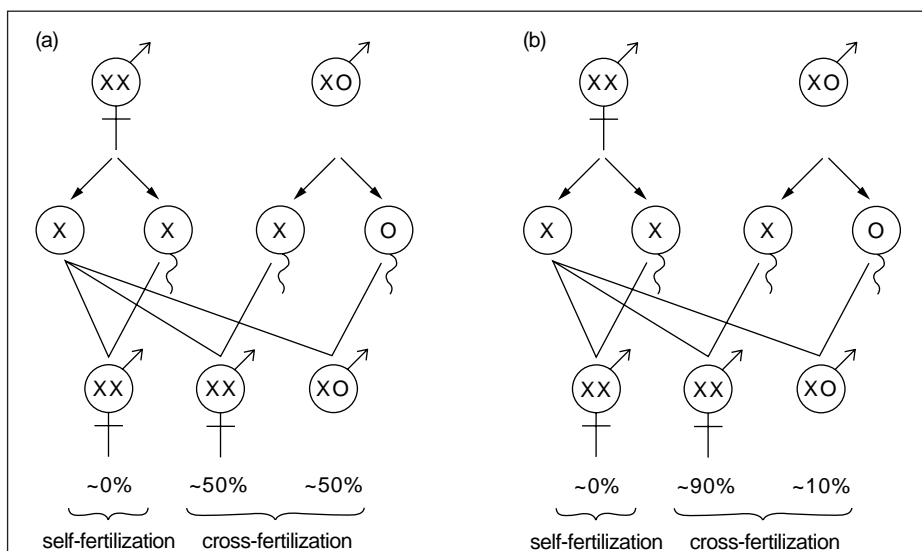

Fig. 1. Gender and parentage of offspring produced within the first 24 h after mating in (a) *Caenorhabditis elegans* and (b) *C. briggsae*. Notice that in *C. elegans*, the X-bearing sperm, as well as the nullo-X sperm from the males, outcompete the sperm from the hermaphrodite. In *C. briggsae*, the X-bearing sperm from the male not only outcompete sperm from the hermaphrodite but also outcompete the nullo-X sperm of the male. Thus, *C. briggsae* gains the benefits of sexual reproduction (outcrossing) without paying the cost of producing males.

subsequently crawl back into the spermatheca to await future ingestion[13].

LaMunyon and Ward have ruled out an alternative explanation for their results – that delayed fertilization is an inherent property of all nullo-X sperm. If this was the case, the interpretation that delayed fertilization represents an adaptation to gain the benefits of sexual reproduction without paying the cost loses much of its strength. Using a mutant *C. briggsae* that produces some nullo-X-bearing sperm (owing to increased nondisjunction), they showed that the nullo-X sperm produced by the hermaphrodite are not inferior to their X-bearing counterparts.

The male X-bearing sperm exclude not only the hermaphrodite sperm, but also the nullo-X sperm of the male. The X chromosome of the male can, therefore, be described as a selfish chromosome because it enhances its own survival at the expense of other chromosomes (present in the nullo-X sperm) in the same individual. However, again, it should be expected that hermaphrodites cooperate in this conspiracy because they can then gain cost-free benefits of sexual reproduction. The selfishness of the X chromosome of the male is only expressed when it passes through a male and not when it passes through a hermaphrodite. Such a phenomenon, in which the same chromosome behaves differently depending on whether it has a paternal or maternal origin, is known as imprinting[14–16].

The selfish X chromosome of *C. briggsae* is reminiscent of the selfish B chromosome of the parasitic wasp *Nasonia vitripennis*[17,18] (which oviposits in the pupae of certain flies). Being a hymenopteran, it follows a haplodiploid life cycle – males develop from unfertilized eggs and are haploid, and females develop from fertilized eggs and are diploid. In some strains, males harbour a B chromosome that has been described as the most selfish genetic element known. The B chromosome confers no known advantage to the male who carries it. Instead, it reaches the zygote via the sperm and inactivates all the paternal chromosomes that have come with it. The diploid zygote, which might have otherwise developed into a female, is thus converted into a male haploid cell consisting only of maternal chromosome (plus the B chromosome) thus ensuring the continued propagation of the B chromosome. The selfish B chromosome of *N. vitripennis* differs from the selfish X chromosome of *C. briggsae* in several ways: the selfish B chromosome destroys its competitor chromosomes, whereas the selfish X chromosome only delays their fertilization; the B chromosome is always selfish, but the selfishness of the X chromosome depends on imprinting; the selfish

B chromosome favours the production of sons, whereas the selfish X chromosome delays or prevents the production of sons; and the selfish B chromosome confers no advantage either to the male that carries it or to the female whose oocyte it enters, whereas the selfish X chromosome confers a clear advantage to the female whose oocyte it enters.

In spite of these differences between the selfish X chromosome of *C. briggsae* and the selfish B chromosome of *N. vitripennis*, their behaviour demonstrates that the broad rules of cooperation and conflict are as applicable to a set of interacting biological molecules as they are known to be to a set of interacting organisms or populations[18,19]. However, it is remarkable that the strategy of *C. briggsae*, which gains all the advantages of sexual reproduction without paying any of the cost of producing males, is not more widespread. Perhaps it comes with a cost that we do not yet appreciate or perhaps it is more widely utilized than we are aware – after all, only a tiny proportion of the described species, let alone the undescribed ones, have been studied to any appreciable degree.

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