

Drosophila Fertilization

Fertilization in *Drosophila* is not your typical type of fertilization. It differs from sea urchin and mammalian fertilization in several ways, and these include

1. Sperm storage by the female
2. The production of enormous sperm by the male
3. Sperm competition based on male-female interactions

Sperm Storage by Female *Drosophila*

In many species, sperm received during mating are kept alive by storing them in sperm storage reservoirs such as the seminal receptacle and spermatheca (see Neubaum and Wolfner, 1999a). In some cases, the sperm are used quickly, while in other instances (such as the eastern box turtle), the sperm can be kept there for years before use. Sperm storage is used by different species for different functions. In some species, it is used to increase fecundity. It allows a female to fertilize hundreds of eggs from a single mating. In other species, sperm storage allows the separation of copulation and fertilization. Mating accomplished in one season can lead to fertilization and development in another. Sperm storage can also allow females to remain fertile over a long duration even though they might not meet males for months or years.

Drosophila melanogaster sperm can be stored by the female for about two weeks, and the sperm in the seminal receptacle are used before those of the spermatheca. (In *Drosophila subobscura*, the reverse is the case and the spermatheca sperm are used first.) Since the sperm reservoirs are usually sacs, it appears that the sperm is used on a "last in-first out" basis (Rothschild, 1991). In *Drosophila melanogaster*, seminal fluid proteins, which are transferred to the female during mating, help mediate the storage, displacement, and release of the sperm. Neubaum and Wolfner (1999b) have identified a seminal fluid protein, Acp36DE, that is critical for sperm storage. Males with loss-of-function mutations in the gene encoding this protein produced and transferred normal amounts of sperm and seminal fluid proteins. However, the females receiving the sperm of these males stored only 15% as many sperm and produced 10% as many adult progeny as control-mated females. Moreover, without Acp36DE, the mated females failed to maintain an elevated egg-laying rate and decreased receptivity, behaviors whose persistence (but not initiation) normally depends on the presence of stored sperm.

Giant Sperm

In 1950, Cooper (quoted in Pitnick et al., 1995) reported that the spermatozoon of *Drosophila melanogaster* "proves to be a most impressive gamete." *D. melanogaster* sperm are indeed large--1.76 mm, about 300 times longer than human sperm (and about as long as the male fly producing them). But even these huge sperm are miniscule compared to the sperm of *Drosophila bifurca*. These sperm are 58 mm long--over 20 times the length of the male fly.

There appear to be trade-offs in the production of these sperm. First, if a fly makes these enormous sperm, it does not make too many of them. Species making smaller sperm make more sperm. Second, the flies making these large sperm have large testes that comprise nearly 11% of the dry mass of the fly. In fact, in *D. hydei* and *D. pachea* (with sperm lengths about 20 mm), the

development of the testes appears to be responsible for delaying the rate of male maturation (Pitnick et al., 1995). In *Drosophila melanogaster*, it appears that the entire sperm enters the egg at the anterior pole and then is seen in the gut region as the embryo develops (Snook and Karr, 1998). The mitochondrial region and flagella are defecated from the early larva. The flagella of the enormous sperm from *D. bifurca* and other such flies does not enter the egg.

Some flies make both short and long types of sperm, but only the long tailed sperm seem to be able to fertilize the egg (Bressac and Hauschteck-Jungen, 1996; Snook and Karr, 1998). The large sperm of *Drosophila* seems to go against the prevailing dogma of behavioral ecology (Krebs and Davies, 1993) that "In all plants and animals the basic difference between the sexes is the size of their gametes: females produce large, immobile, food-rich gametes called eggs, while male gametes or sperm are tiny, mobile, and consist of little more than a piece of self-propelled DNA." Here, it seems like the nucleus is more like a tennis ball on the tip of a skyscraper. The entire sperm (tail and all) gets incorporated into the oocyte cytoplasm, and the sperm cell membrane does not break down until after it is fully inside the oocyte (Snook and Karr 1998; Clark et al. 1999).

Sperm Competition

In *Drosophila melanogaster*, females will mate before their stored sperm is used up. This means that the sperm storage reservoirs in the female usually contain sperm from more than one male. Different genotypes of sperm appear to compete better, and different genotypes of females differ widely in their adherence to the general "last in-first out" principle (Clark et al., 1995; Hughes et al., 1997). It also appears that one genotype of sperm is not the "victor" of such competitions in all genotypes of females (Clark et al., 1999). Some sperm compete better in some females than in other females. (No sperm competition has been observed in humans—despite various hypotheses saying that it exists and should be expected. See Moore et al., 1999, for details).

Fertilization does not occur until the eggs are about to be laid. At that time, the sperm storage reservoirs emit a few sperm as each egg passes down the oviduct. The orientation of the egg in the oviduct probably facilitates sperm entry. In *Drosophila*, the micropyle of the egg (that single hole in the chorion at the anterior end of the egg through which sperm can pass) comes opposite the ventral receptacle of the oviduct, which contains stored sperm. It is usual for only one or a few sperm to enter the egg (Chapman, 1982). Very little is known about sperm/egg binding or fusion in *Drosophila*. Similarly, the blocks to polyspermy are not known, although like other yolky eggs, multiple sperm might be allowed entrance into the cytoplasm, but only one will survive (Loppin et al 2015)

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