Evolutionarily dynamic sperm

Evolutionary biologists really got interested in sperm only after the realization that if more than one male inseminates a female, males are not passive recipients of sperm. A classic example of a male mating strategy that benefits females, and females attempt to avoid males to considering the roles of both sexes, their conflicting interests and the evolutionary consequences of everything that goes on between copulation and fertilization. The 5th Biology of Spermatozoa meeting echoed the field’s broadening horizons and its fundamental role in understanding sexual selection.

Instead of regarding females as passive receptacles for sperm, the dominant paradigm is now to regard interactions between the sexes as an ongoing conflict. Males attempt to inseminate as many females as possible and females attempt to avoid males and have their own sperm stored in the body cavity from where it migrates to the reproductive tract. The magnitude of this discrepancy between males and females is substantially reduced if the semen from multiple males is inseminated into the female. The process can be seen in action in multigenerational lines of D. melanogaster, in which one of the males has already inseminated a female (polyandry), and the other pair has females kept with a single male (monandry). Both strategies have been investigated by Brett Holland (University of California, Lafayette, USA) described how, after 32 generations, males from the monandrous line are more benign when mated to test females and also court less readily. Similarly, monandrous-line females suffered more when mated to a test male than polyandrous females, indicating that they had lost some of their resistance to toxic effects of male ejaculates. Both results indicate that within a few generations both sexes adapt to a reduction in sperm competition. Holland has passed his selected lines on to Scott Patnick (University of Syracuse, NY, USA), who is investigating differences in sperm competitive ability between the lines. Although this work is ongoing, it is already apparent that males from the polyandrous line are more successful when sperm are in competition with those of a previous male than are males from the monandrous line. The reduction in sperm-competition ability in monandrous males suggests that success in sperm competition has costs, either directly or through reducing female fecundity.

The generality of costs of sperm competition to both sexes found in D. melanogaster could be investigated by comparing patterns of male-female interactions across populations or species of other taxa. However, it was pointed out by Geoff Parker (University of Liverpool, UK) that even rare polyandry (as tends to be found in apparently monogamous species) theoretically is predicted to create similar selection pressures on males as rampant polyandry. This suggests that differences between completely monandrous and polyandrous selection lines might not be seen between populations differing in their degree of polyandry in natural situations.

As well as adapting to male sperm-competitive tactics, there is growing evidence that females exercise considerable control over inseminated sperm, and might even actively choose to fertilize their eggs with sperm from particular males. An example of such behaviour has been studied by Tommaso Pizzari (University of Sheffield), who showed that female feral chickens can not only physically eject inseminated sperm, but that they do so more frequently when inseminated by a lower ranking male. However, chickens might be out-done by bed bugs (Cimex lectularius). In this species, males pierce the female body wall and inject sperm directly into her body cavity from where it migrates to the ovaries. Alastair Stutt (University of Sheffield, UK) has found, as might be expected, that this makes mating costly, with females exposed to more matings having substantially reduced lifespans. Of course, females are not passive victims of aggressive male strategies – sexual conflict drives coevolution between males and females. This process can be seen in action in multigenerational lines of D. melanogaster, in which one pair of lines has females kept with four males (polyandry), and the other pair has females kept with a single male (monandry). Both strategies have been investigated by Brett Holland (University of California, Lafayette, USA) described how, after 32 generations, males from the monandrous line are more benign when mated to test females and also court less readily. Similarly, monandrous-line females suffered more when mated to a test male than polyandrous females, indicating that they had lost some of their resistance to toxic effects of male ejaculates. Both results indicate that within a few generations both sexes adapt to a reduction in sperm competition.

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same species indicates that sperm traits might be under directional selection. Females inseminated with a mixture of sperm from two males differing only in sperm mobility had more of their eggs fertilized by the male with higher mobility sperm. If mobility differences are due to mitochondria, then selection will favor males with particular mitochondrial genotypes. This might be successful in fertilizing eggs, none of their offspring will inherit this characteristic. Therefore, mitochondrial inheritance provides a potential explanation for the maintenance of variation in a directionally selected trait.

Overall, the meeting clearly demonstrated that our current understanding of the role of postcopulatory processes is just the tip of the iceberg. To have any hope of understanding the extravagant world of sexual selection, we must consider the world of the sperm.

Testosterone and maternal effects – integrating mechanisms and function

One hundred and twenty-eight years after Darwin first described the two processes of sexual selection – male–male competition and female choice – the latter component continues to cause controversy. The main debate lies in those cases, such as lekking species, where females apparently obtain nothing but semen from the male with which they copulate. In such species, males contribute no paternal care, and thus it is assumed usually that females obtain only indirect or genetic benefits from their choice of partner. Consequently, female choosiness in return for no obvious benefit is referred to as the ‘lek paradox’. Several different types of genetic benefit are plausible, but the one that has attracted the most interest is the idea of viability genes. This ‘good genes’ hypothesis has been difficult to test, but there is now some evidence for it because several studies have reported increased viability of offspring fathered by attractive males. Researchers testing the good genes hypothesis have had to be careful to avoid confounding maternal effects. For example, over ten years ago, it was shown that within pairs of zebra finches (Taeniopygia guttata), females paired to attractive males invested more in offspring than females paired to less attractive males; this raised the possibility that any increase in the viability of offspring fathered by attractive males could be due to either a maternal effect (increased investment by the mother), to the father’s ‘good genes’ or, more probably, to both (given that females are expected only to invest more if they increase their fitness). Several studies looking for good genes effects in birds have attempted to control for maternal effects; for example, by hatching eggs in incubators, but, of course, this does not preclude the possibility of differential maternal investment before egg-laying. A new study of zebra finches by Gil et al. has shown that one maternal effect in particular – the amount of testosterone deposited in eggs – could have a profound influence on a female’s offspring, in a way that varies according to the attractiveness of her mate.

Gil et al. found that in captivity female zebra finches deposit relatively more of the androgens testosterone and 5α-dihydrotestosterone into their eggs when paired to an attractive male. They were able to demonstrate this in a particularly elegant manner, because the attractiveness of male zebra finches (Fig. 1) can be manipulated by the addition of colour-rings – red rings render males more attractive and green rings reduce male attractiveness. Gil et al. looked at androgens in the eggs of females paired to the same males wearing red or green rings in different clutches. Females put significantly more androgens into their eggs when their male social partner wore red rings compared with when the same male wore green rings. In canaries, Serinus canaria, a higher level of androgens in the eggs gives chicks of both sexes a head start in several ways – in the nest they beg more and grow faster, and they have higher social rank once fledged. Gil et al. assume that similar advantages would accrue in zebra finches hatching from high androgen eggs. With these advantages, why don’t females put similar amounts of androgens into all eggs regardless of their partner’s apparent quality? Gil et al. suggest that androgens might be costly, either to the mother or to her offspring; for example, by suppressing the immune system. They propose also that only offspring fathered by genuinely high-quality males would be able to withstand the high concentration of androgens. There are other potential costs not mentioned by Gil et al.; for example, although increased growth might provide short-term benefits, other studies of zebra finches indicate that it can result in reduced subsequent survival.

These remarkable results raise several other questions. The zebra finch is a socially monogamous species, but (in common with many other passerine birds) also engages in extra-pair copulations (EPCs), which result in extra-pair paternity...