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INVITED RESEARCH HIGHLIGHT

Sperm Biology

Quantity versus quality: the sperm war

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The evolution of sperm traits manifests itself prolifically across species, and postcopulatory sexual selection (PSS), as executed by the female, accompanies this process. The adaptive significance of some sperm traits (for example, the shape and number of sperms) is well understood. However, the evolution of germ size has not been fully exploited. The most recent study by Lüpold *et al.*[1] reveals that the evolution of longer sperm is driven by the female seminal receptacle and mating frequency in *Drosophila*, which, in turn, increases the benefits to females. These findings provide a comprehensive interpretation regarding the evolution of sperm size.

Male sexual traits have evolved more rapidly than other types of characteristics.[2,3] For example, it is well known that antlers, horns, tail feathers, mandibles, and dewlaps are exaggerated ornaments related to reproduction and that natural selection is the driving force behind this rapid evolution.[4,5] Sexually antagonistic (precopulatory sexual selection) and postcopulatory sexual selection are the two main reasons responsible for this evolutionary pattern.[6]

Sperms are highly specialized cells for transferring genetic information from the male to female egg. Although the process of spermatogenesis (*i.e.,* meiosis and the sperm maturation process) is highly conserved across different taxa, sperm morphology shows great variation.[7,8] Variation in sperm tail length is of particular interest, and a positive relationship between sperm size and sperm competition has been established for different organisms such as birds, butterflies, and fruit flies.[2,3] A coevolution of the female reproductive tract and sperm length has also been identified.[9] Extensive studies show that PSS mediated by female preference drives this evolution and that female morphology, physiology, and behavior that are observed after coupling contribute to this preference.[6,10]

Drosophila species have the most variable sperm length.[11,12] For example, the gigantic sperm of *D. bifurca* is over 58 mm in length, approximately 20 times the total body length of males. And this giant sperm may represent the most extreme germ cell in the animal kingdom with respect to size.[13] Given a wealth of cellular and molecular tools, the highly conserved gametogenesis between flies and mammals, and the ease of genetic manipulation, *Drosophila* has emerged as an important model system for the study of sperm tail length and female interactions.[14] By experimentally manipulating *D. melanogaster* populations, the authors previously established different fly lines showing either increased or decreased sperm lengths or length of the female's primary sperm storage organ, the seminal receptacle (SR).[9] Careful examination of these lines showed that giant sperm tails are the cellular equivalent of the peacock's tail, and that female preference (SR length) drives the evolution of sperm length. Although the functional relationship between female preference and the corresponding male ornament is unambiguous, how sexual selection drives the evolution of costly sperm ornamentation remains unclear.[6]

In their most recent paper, Lüpold *et al.*[1] extended their previous work and further evaluated the genetic and phenotypic correlations, as well as heritabilities in sperm length, SR length, remating day, ejection time, and the proportion of resident spermatozoa that are thoroughly displaced within diallel crosses. Consistent with their previous study, they found that a highly significant, positive genetic correlation exists between sperm and SR length. They further showed that this positive genetic correlation between sperm and SR length serves to drive both sperm length and SR length coevolution. Assessing other sexual traits, these authors surprisingly discovered that SR length was genetically negatively correlated with the female remating interval, but positively correlated with the ejection time. Thus, increases in SR length would further intensify directional selection of sperm length. Collectively, these results suggest that the few gigantic sperm evolved by Fisherian runaway selection through genetic correlations among sperm length, female preference, and female mating frequency.

Giant sperm may manifest great advantages in fertilization, but we then ask, "Do they provide genetic benefits to the female as a reliable indicator of male quality? And if so, how are these benefits to be gained?" To answer these critical questions, the authors assessed the sensitivity of sperm length relative to the nutritional history and the physiologic condition of males using a quantitative genetic assay in *D. melanogaster*. They found that sperm length was highly heritable, but that it was not condition dependent. In contrast, sperm number was dependent upon nutrition or other conditions. Therefore, it may be interesting to infer that sperm length evolution may be correlated with its influence on the condition dependence of sperm number. Investigations of seven *Drosophila* species further demonstrated that males of any condition can produce many "cheap" sperm and inseminate oocytes them with, but only high-quality males have the available resources to produce abundant "expensive" sperm. Therefore, through the indirect control of sperm quantity by their "quality," the numbers of giant sperm have become a reliable indicator of overall male quality.

Both sperm quality (length) and quantity (number) contribute to competitive

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fertilization success and relative fitness. From a series of publications on giant sperm evolution, the Pitnick laboratory has offered a comprehensive resolution to the big-sperm paradox by revealing an interacting combination of trait covariance and mating-system characteristics.[1,6,9,13] On the one hand, poor-quality males may pay higher costs for the production of plentiful long sperm; however, on the other hand, females of species with longer SRs remate more frequently, depleting sperms more rapidly. The strong positive relationship between sperm length and the female-specific opportunity for sexual selection is thereby determined, and the cryptic female choice then shapes the evolution of sperm form.

In vitro fertilization (IVF) is an artificial technology in which an oocyte is fertilized by sperm outside the body, and IVF has been widely used to overcome female or male infertility in humans.[15] Compared to natural fertilization, the PSS is largely absent in IVF, but artificial selection is greatly enhanced. Given that PSS is responsible for the rapid evolution of sperm quality traits across diverse taxa, it may be interesting to investigate the alteration in sperm quality traits within a population born after IVF.

COMPETING INTERESTS

Both authors declared no competing interests.

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