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INVITED RESEARCH HIGHLIGHT

Sperm Biology

The long and the short of it: new insights on sperm length help demystify the complexities of sexual selection

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Human sperm are approximately 6000th of a centimeter long, a small fraction of a man's total body length. By contrast, fruit fly (*Drosophila* spp.) sperm can reach nearly 6 cm, roughly twenty times the total length of their bodies. This dramatic variation in male reproductive biology is explored in a recent paper from the journal *Nature*.¹ While the literature on sperm competition has for decades emphasized the fitness benefit males of many species accrue by producing small gametes in large quantities, understanding species whose males produce large gametes in small quantities while remaining competitive for fertilizations has until recently proven more difficult. Stefan Lüpold and colleagues suggest a solution to this “big-sperm paradox.”

Most sexually reproducing organisms exhibit two discrete sexes, defined by the type of gamete they produce: males produce many small sperm while females produce fewer, but larger, ova. As such, the number of ova constrains the possible number of offspring that can be conceived. In turn, males must often compete for mates² and consequently exhibit greater variance than do females in the number of offspring they are able to produce; some males manage many mating partners, others none.³ This competition drives sexual selection,⁴ the type of evolution via natural selection favoring traits that aid their bearers in winning mating opportunities, thus increasing their reproductive fitness. An outcome of this process is the well-documented cross-species sex difference of greater male

competitiveness for mating opportunities⁵ and interest in unfamiliar mates.⁶ As a result, male phenotypes frequently appear molded by sexual selection to a greater degree than do female phenotypes.⁵

While sexual selection shapes traits that mediate access to mates, the process does not end with copulation.⁷ In many species, particularly those in which it is difficult for males to monopolize sexual access to females, rival male gametes compete to fertilize ova once copulation has occurred. This postcopulatory process, a mechanism of sexual selection known as sperm competition, results in variation in sperm number, morphology, and motility.⁸ Because males are the sex that competes in this way for reproduction, it is of little surprise that testis size is a correlate of sperm production in mammals,⁹ who also exhibit larger relative testis size in species with promiscuous female mating.¹⁰ Moreover, while sexual selection is likely to favor any male trait that enhances the prospect of fertilization, such as vasa deferentia better at sperm transport,¹¹ increased sperm quantity seems to be the route taken by males of myriad taxa.

How, then, are we to understand the massive sperm seen in some insects, particularly in light of the tradeoff between size and quantity inherent to the production of sperm? Since the difference in gamete size is thought to be the ultimate driver of sex differences,⁵ species in which males produce relatively few large sperm, thus displaying a decrement in the number of rival gametes, should be more weakly influenced by sexual selection. Among fruit flies (*Drosophila* spp.), for instance, species that produce longer sperm tend to produce fewer,¹² yet exhibit

competition among males nonetheless. This phenomenon has come to be known as the big-sperm paradox,^{1,13} and Lüpold *et al.* suggest a solution to it: runaway sexual selection.

Proposed by biologist Ronald Fisher,¹⁴ runaway sexual selection posits a genetic coupling of female preferences with male traits. The process is thus putatively responsible for conspicuous male ornamentation such as red coloration in the three-spined stickleback (*Gasterosteus aculeatus*), a species of fish among whom sons' intensity of red coloration is positively related to daughters' preference for redness in mates.¹⁵ Such male traits may confer some type of initial survival advantage, with females who happen to choose them tending to produce better-surviving sons possessing the traits as well as daughters with a preference for them.⁵ This creates a positive feedback loop: as more females in the population mate with more intensely red-colored males, the reproductive fitness of males with the trait and females with a preference for the trait increases.

Sperm, argue Lüpold *et al.*, may in some species represent an example of runaway sexual selection. Because male traits exhibit heritable variation, female reproductive fitness is contingent on mating with males able to provide offspring with the best genes,¹⁶ and one means by which females discriminate among prospective mates is male–male competition. A criterion females use as an indication of male quality in some species of fruit fly may be sperm length, with postcopulatory competition facilitated by females' ability to store male gametes in large seminal receptacles whose energetic cost is outweighed by the increased

likelihood of fertilization with high-quality sperm. To that end, Lüpold *et al.* show that larger seminal receptacles in *Drosophila melanogaster* are related to female mating frequency and increased selective ejection of sperm from the reproductive tract, both of which increase postcopulatory competition. A similar situation is present in mammals, among whom increased oviduct length is associated with larger testes.¹⁷ Moreover, as Lüpold *et al.* report, the genes that cause fruit fly mothers to have larger seminal receptacles cause longer sperm in their sons, a finding consistent with runaway sexual selection. The difference between fruit flies and mammals, however, is that male reproductive success in the former tends to be contingent on gamete quality and in the latter gamete quantity.

Why the difference, though, between these phylogenetically distant taxa? Why do *Drosophila* males deviate from the commonly seen negative relationship between gamete size and quantity? The answer, Lüpold *et al.* suggest, may have to do with development: while stressful rearing conditions in their study had no impact on sperm length, they were associated with diminutive body size. This suggests that only high-quality males are able to produce these large sperm in greater numbers, thus increasing their likelihood of fertilization. The finding, moreover, accords with prior research showing greater fertilization success for longer *D. melanogaster* sperm, which may be produced by displacement of rival male gametes.¹⁸

Lüpold *et al.* thus put forth a parsimonious interpretation of fitness benefits accrued by both sexes: fruit fly females prefer larger sperm, which males therefore must and do possess. More than provide merely a new example of the Fisherian runaway process, however, this research (a) demonstrates the salience of sexual selection in species exhibiting greater parity in gamete size, (b) highlights large sperm as a male strategy for fitness maximization in some species, and (c) recognizes the artificiality of treating sperm competition and mate choice as

unique mechanisms of sexual selection. These contributions notwithstanding, Lüpold *et al.*'s work may not have great relevance to the study of humans since sperm length and relative testis size appear largely unrelated in mammalian males,¹⁹ who are reproductively advantaged by greater quantities of gametes.⁹ One explanation for this may be that larger sperm can more easily displace rivals in smaller-bodied organisms such as fruit flies than they can in larger-bodied organisms.²⁰ Additionally, because testis maintenance requires a larger percentage of energetic resources in smaller species (e.g., in mammals¹⁰), production of large sperm may serve as an indication of underlying male quality in smaller species. Humans, though, are a large species whose males possess relatively small testes²¹ alongside a host of traits suggestive of an evolutionary past characterized largely by premating competition, particularly physical aggression or threats of physical aggression.²² By helping to unravel the big-sperm paradox, however, Lüpold *et al.*'s important contribution to the literature provides further evidence of the diverse directions sexual selection can take. It thus informs our understanding of the often bewildering differences exhibited by males and females, whose vastly divergent ways of competing for reproduction prompted the evolutionary biologist Robert Trivers to suggest that the sexes be treated as separate species.²³ As Lüpold *et al.* demonstrate, Trivers seems to have been right.

COMPETING INTERESTS

Both authors declared no competing interests.

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