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 length of their bodies. This dramatic variation in male reproductive biology is explored in a recent paper from the journal Nature. 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 mates 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. This competition drives sexual selection, 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 opportunities and interest in unfamiliar mates. As a result, male phenotypes frequently appear molded by sexual selection to a greater degree than do female phenotypes.

While sexual selection shapes traits that mediate access to mates, the process does not end with copulation. 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. 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, who also exhibit larger relative testis size in species with promiscuous female mating. 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, 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, 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, yet exhibit competition among males nonetheless. This phenomenon has come to be known as the big-sperm paradox, and Lüpold et al. suggest a solution to it: runaway sexual selection.

Proposed by biologist Ronald Fisher, 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. 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. 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, 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. 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.

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 unrelated in mammalian males, who are reproductively advantaged by greater quantities of gametes. 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. Additionally, because testis maintenance requires a larger percentage of energetic resources in smaller species (e.g., in mammals), 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 testes alongside a host of traits suggestive of an evolutionary past characterized largely by preying competition, particularly physical aggression or threats of physical aggression. 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. As Lüpold et al. demonstrate, Trivers seems to have been right.

COMPETING INTERESTS
Both authors declared no competing interests.

REFERENCES
1 Lüpold S, Manier MK, Puniamoorthy N, Schoff C, Starmer WT, et al. How sexual selection can drive the evolution of costly sperm ornamentation. Nature 2016; 533: 535–8.
2 Emlen ST, Oring LW. Ecology, sexual selection, and the evolution of mating systems. Science 1977; 197: 215–23.
3 Bateman AJ. Intra-sexual selection in Drosophila. Heredity 1948; 2: 349–68.
4 Clutton-Brock TH, Parker GA. Potential reproductive rates and the operation of sexual selection. Q Rev Biol 1992; 67: 437–56.
5 Andersson MB. Sexual Selection. Princeton, NJ: Princeton University Press; 1994.
6 Wilson JR, Kuehn RE, Beach FA. Modification in the sexual behavior of male rats produced by changing the stimulus female. J Comp Physiol Psychol 1963; 56: 636–44.
7 Parker GA. Sperm competition and its evolutionary consequences in the insects. Biol Rev 1970; 45: 525–67.
8 Inmiller S, Moore HD, Breed WG, Birkehead TR. By hook or by crook? Morphometry, competition and cooperation in rodent sperm. PLoS One 2007; 2: e170.
9 Maller AP. Ejaculate quality, testes size and sperm production in mammals. Funct Ecol 1989; 3: 91–6.
10 Kenagy G, Trombulak SC. Size and function of mammalian testes in relation to body size. J Mammal 1986; 67: 1–22.
11 Anderson MJ, Nyholt J, Dixon AF. Sperm competition affects the structure of the mammalian vas deferens. J Zool 2004; 264: 97–103.
12 Pitnick S. Investment in testes and the cost of making long sperm in Drosophila. Am Nat 1996; 148: 57–80.
13 Bjørk A, Pitnick S. Intensity of sexual selection along the anisogamy-isogamy continuum. Nature 2006; 441: 742–5.
14 Fisher RA. The Genetical Theory of Natural Selection. Oxford, UK: Clarendon Press; 1930.
15 Bakker TC. Positive genetic correlation between female preference and preferred male ornament in sticklebacks. Nature 1993; 363: 255–7.
16 Petrie M. Improved growth and survival of offspring of peacocks with more elaborate trains. Nature 1994; 371: 598–9.
17 Anderson M, Dixon A, Dixon A. Mammalian sperm and oviducts are sexually selected: evidence for co-evolution. J Zool 2006; 270: 682–6.
18 Lüpold S, Manier MK, Berben KS, Smith KJ, Daley BD, et al. How multivariate ejaculate traits determine competitive fertilization success in Drosophila melanogaster. Curr Biol 2012; 22: 1667–72.
19 Gage MJ, Freckleton RP. Relative testis size and sperm morphometry across mammals: no evidence for an association between sperm competition and sperm length. Proc R Soc Lond B: Biol Sci 2003; 270: 625–32.
20 Immler S, Pitnick S, Parker GA, Durrant KL, Lüpold S, et al. Resolving variation in the reproductive tradeoff between sperm size and number. Proc Natl Acad Sci 2011; 108: 5325–30.
21 Anderson MJ, Dixon AF. Sexual selection affects the sizes of the mammalian prostate gland and seminal vesicles. Curr Zool 2009; 55: 1–8.
22 Hill AK, Bailey DH, Puts DA. Gorillas in our midst? Human sexual dimorphism and contest competition in men. In: Tibayrenc M, Ayala FJ, editors. On Human Nature: Biology, Psychology, Ethics, Politics, and Religion. New York, NY: Academic Press. [In press].
23 Trivers R. Parental investment and sexual selection. In: Campbell BG, editor. Sexual Selection and the Descent of Man, 1871-1971. Chicago, IL: Aldine de Gruyter; 1972. p. 136–79.