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Evolution: The Paradox of Sperm Leviathans

Sexual selection theory predicts that sperm competition will push males to produce more, smaller sperm. Paradoxically, in the fruitfly *Drosophila bifurca* sperm competition is rife but males produce few, giant sperm — the largest known. A recent study reconciles the evolution of giant sperm with theory.

Tommaso Pizzari

The evolution of sexual reproduction typically leads to frequency-dependent disruptive selection on gamete size and numbers, promoting two strategies: large eggs that nurture and protect the embryo and are little mobile; and tiny, mobile, self-propelled, DNA-delivering sperm, which are able to seek out and fertilize eggs [1]. Such sex-specific differential investment in gametes is called anisogamy, and sets the scene for the way sexual selection operates [2–4]. Males, which produce far more sperm than there are eggs available, have a higher potential reproductive rate than females. This means that male reproductive success will be more variable than female reproductive success, leading to more intense sexual selection on males than on females.

In 1948, Bateman [5] demonstrated the implications of anisogamy through an elegant experiment in the fruitfly *Drosophila melanogaster*. Bateman showed that male reproductive success increases with the number of females with whom a male copulates, whereas female reproductive success is largely independent of her re-mating rates. These results indicated that the main reason for why male fitness is more variable than female fitness is that males vary more than females in the number of partners, leading to more intense sexual selection on male re-mating rates.

Anisogamy may be further increased by the fact that, in many species, females mate with multiple males — they are polyandrous — and the ejaculates of different males compete over fertilization [6,7]. Here, sexual selection continues after insemination through sperm competition, and because larger ejaculates tend to have a fertilizing advantage [8,9], and a trade-off exists between sperm number and size [10,11], males are sexually selected to produce numerous, tiny sperm [10].

There is widespread support for this theoretical prediction. In a number of taxa, males of polyandrous species, where sperm competition is intense, invest a larger proportion of their body mass in testes to produce sperm at a faster rate than males

of related monandrous species [7,12–14]. With this in mind, it would seem paradoxical that the largest known sperm in the animal kingdom are found in the tiny males of a polyandrous fly where sexual selection and sperm competition appear rife. Males of the fruitfly *Drosophila bifurca* produce very few, giant sperm that are just under six centimetres long [15] (Figure 1). How did this extreme, female-like gametic strategy evolve in a species where sexual selection appears intense?

In a monumental recent study, Adam Bjork and Scott Pitnick [16] set out to unravel the evolutionary paradox of giant sperm using a two-pronged approach. First, they capitalised on the high diversity of male investment in sperm size and numbers across *Drosophila* species, and replicated Bateman's classic experiment on four different *Drosophila* species which vary markedly in sperm size: *D. melanogaster*, *D. virilis*, *D. lummei* and *D. bifurca*. *D. melanogaster* have relatively small sperm (1.87 millimetres) and are anisogamous, whereas at the opposite end of the gradient, *D. bifurca* is as close as *Drosophila* – or any known metazoan species – get to an equal investment per male and female gamete (isogamy). Second, the authors were able to replicate the study in lines of *D. melanogaster* that were experimentally and divergently selected for long and short sperm, which enabled them to study the causal relationship between sperm size and sexual

selection that was detected in their comparative analysis.

Bjork and Pitnick [16] confirmed Bateman's original results that male reproductive success is dependent on male re-mating rates (a measure of the number of females mated), while female reproductive is to a large extent independent of female re-mating rates. But they found revealing differences associated with sperm size. In the more anisogamous *Drosophila* species, *D. melanogaster* and *D. virilis*, female reproductive success was constant over female re-mating rates, while male reproductive success increased significantly with male re-mating rates. However, in the *Drosophila* species that approach isogamy because males produce few egg-like giant sperm, *D. lummei* and *D. bifurca*, there was a trend for both male and female reproductive success to increase with re-mating rates. Furthermore, consistent with the idea that sperm gigantism is associated with relatively intense sexual selection, sperm size was closely positively correlated with proportional testis mass across these species. Therefore, *D. lummei* and *D. bifurca* males invested proportionally more body mass in gonads, but they used their large gonads to produce few, giant sperm rather than more, smaller sperm. Importantly, a strikingly similar pattern was observed across *D. melanogaster* lines selected for long and short sperm.

To understand better how selection operates differentially on male and female re-mating, Bjork and Pitnick [16] analyzed the relative intensity of sexual selection on male re-mating in two ways. First, they measured the slope of the regression of reproductive success over re-mating rate, and quantified the difference between the male and the female slope in each species and selection line. They found a significant decline in slope difference across species with progressively larger sperm. Once again, the same trend was confirmed by the comparison of artificially selected *D. melanogaster* lines. This decline was not due to selection on male re-mating being weaker on males producing
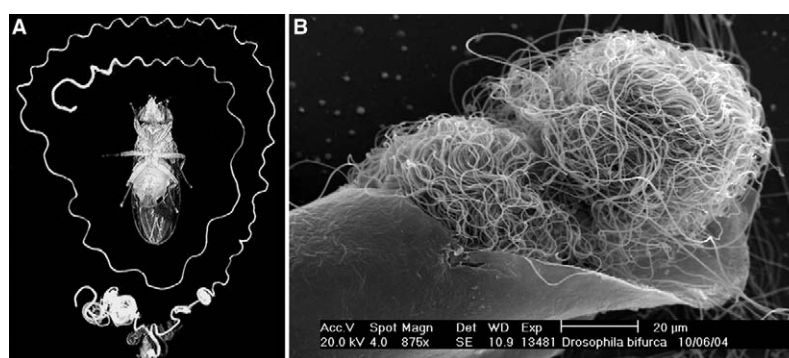

Figure 1. The largest sperm known.

(A) Male *Drosophila bifurca* surrounded by his own testis. A male was photographed before he was dissected, and his uncoiled left testis subsequently photographed at the same magnification (photo, Scott Pitnick). (B) Two spermatozoa within the male's seminal vesicle. (Photo, Romano Dallai.) A recent study [16] sheds light on how sexual selection may promote the evolution of such sperm giants.

large sperm, but rather, to selection on female re-mating becoming more pronounced in large sperm species and *D. melanogaster* selection lines.

Second, the authors also quantified sexual selection as the opportunity of sexual selection (I_s), a dimensionless index of the strength of sexual selection derived from the difference of the opportunity of selection on females ($I_{females}$ = variance in female reproductive success/(mean female reproductive success)^2, when the number of males equals the number of females in a population) and on males (I_{males}) [4]. Contrary to the slope difference, the opportunity of sexual selection did not decrease with increasing sperm size. In fact, if anything the opportunity of selection on males increased more than that on females, resulting in a non-significant trend for I_s to increase with sperm size. Together, these results indicate that in species with large sperm, sexual selection on male re-mating is relatively strong, but this may be masked by the fact that selection on female re-mating may also be more pronounced than in species producing more and more conventional sperm.

One possibility for the high opportunity of selection is that giant sperm are associated with relatively high variance in male and female reproductive success. Previous experimental work by the same group [17] demonstrated, through experimental evolution in

D. melanogaster, that sperm size is driven by the evolution of the female sperm-storage organ morphology. When females have large sperm-storage organs, they may bias the outcome of sperm competition in favour of longer sperm (a process called cryptic female choice). In other words, exaggerated sperm tails may be the 'post-copulatory equivalent of peacock trains' [17]. When males produce few giant sperm, however, the variance in paternity may be higher, as some ejaculates may miss out completely on paternity shares.

Similarly, when females copulate with few males, each inseminating few giant sperm, some of the eggs may fail to be fertilized, resulting in high variance in female reproductive success. This would explain why the slope of female reproductive success over re-mating tends to be positive and as steep as that of male reproductive success in giant sperm species [16]. It is therefore possible that sexual selection, through sperm competition and cryptic female choice, drives the evolution of male investment in few, giant sperm. But, the larger and fewer the sperm produced, the more variable female and, especially, male reproductive success becomes, leading to reinforcing sexual selection on sperm size. In other words, once females (or some mechanism of sperm competition) begin to bias paternity in favour of larger sperm, the direction of post-copulatory

sexual selection may be reversed: from the traditional strategy of producing many tiny sperm, fostering anisogamy, to the production of ever larger, ever fewer sperm, a counterintuitive runaway from anisogamy.

The new work of Bjork and Pitnick [16] indicates that, when sperm size plays an important role in sperm competition, the evolutionary trajectory of sperm traits under sexual selection is more difficult to predict. This may shed new light on recent studies showing that sperm competition may sometimes favour the production of longer [17–19] or larger [20] sperm, not necessarily of more sperm.

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Animal Cognition: Monkey Meteorology

Mangabey monkeys have been shown to rely on memory of recent trends in temperature and solar radiation to decide whether to feed on a particular patch of fruit. These observations reveal a rich mental representation of the physical environment in monkeys and suggest foraging may have been an important selective pressure in primate cognitive evolution.

Michael Platt

People love to talk about the weather, and not just because it provides an easy entrée into conversation. Weather forecasts help us to plan our days, elect to wear a heavy coat or take along an umbrella, decide when to plant our crops, or scrub a planned spacecraft launch. Their utility is evident in the earliest written documentation of weather patterns by the ancient Greeks and Chinese over 2000 years ago (for example, Aristotle's *Meterologica*). Incised bone fragments from the Paleolithic may track the lunar cycle, raising the possibility that even pre-historic humans kept astronomical records useful in forecasting the weather [1]. Even today, the Weather Channel remains an exceptionally popular media outlet, reaching over 89 million households in the U.S. and consistently ranked in the top 15 of all web sites, despite inevitable inaccuracies in forecasting even with modern meterological methods.

But is this fascination with the weather uniquely human? After all, weather information would appear to be equally useful for animals, for example in planning group movements [2] or timing reproduction [3]. A particularly compelling problem confronting many animal species is choosing where to forage for food. It seems reasonable to suppose that foraging decisions could be improved by taking weather into account, as the quantity and quality of many foods is strongly influenced by recent meteorological trends [4]. In savannah habitats, for example, rainfall patterns largely determine the availability of ripe fruits [4], whereas consistently warm seasonal temperatures lower the nutritional quality of grasses [5].

Despite the obvious utility of meteorological information for guiding foraging decisions, conclusive evidence for its use by animals remains elusive. Prior studies have demonstrated that current weather conditions influence behavior, for example when animals seek shade during the midday heat or huddle together when cold, and that activity patterns in general can be indirectly influenced by the affects of weather on food availability [4]. In this issue of *Current Biology*, Janmaat *et al.* [6] provide compelling new evidence that monkeys actually make decisions