Digest: Evolution of sperm size and number in external fertilizers

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This article corresponds to Liao, W. B., Y. Huang, Y. Zeng, M. J. Zhong, Y. Luo, and S. Lüpold. 2017. Ejaculate evolution in external fertilizers: Influenced by sperm competition or sperm limitation? *Evolution*, doi: 10.1111/evo.13372. http://onlinelibrary.wiley.com/doi/10.1111/evo.13372/full

Abstract

Ejaculate evolution in externally fertilizing species is influenced by competition among sperm as well as the rate at which sperm and eggs encounter one another. Liao et al. (2017) found that ejaculate evolution in external fertilizers depended on spawning conditions. In anurans, gametes are released very close to eggs and are relatively protected from dispersal by water currents, thus sperm competition is more important. However, in fish, sperm-egg encounter rate plays a much more important role in ejaculate evolution because gametes may be easily dispersed when released into the aquatic environment.

Digest

Evolution of gamete size and number is a crucial aspect of the evolution of anisogamy (reproduction with unequally-sized gametes). For decades, evolutionary biologists have asked how isogamous ancestral forms evolved anisogamy and oogamy (unequally-sized gametes in which the small gametes are more abundant and motile than the large gametes) (Togashi and Cox 2011). To date, answers to this question derive largely from theoretical models (Parker et al. 1972; Bell 1978; Charlesworth 1978; Togashi and Cox 2011; for a review, see Lessells et al. 2009). These models can be categorized into three different classes, where each class recognizes a unique set of selection pressure(s) as the evolutionary force selecting for and maintaining anisogamy. These selection pressures were identified by Lessells et al. (2009) as i) gamete competition, ii) sperm limitation, and iii) intracellular conflict. Lessells and colleagues concluded that the most robust models are those predicated on gamete competition, in particular the one proposed by Parker, Baker, & Smith (1972) (often abbreviated as the PBS theory or model, e.g. Bell (1978)).

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Evolution of sperm size and number is generally assumed to be rooted in an intrinsic trade-off between the size and the number of gametes (Parker et al. 1972; Lessells et al. 2009 and references within). Because available resources are usually limited, the number of gametes produced should be inversely proportional to their size.

Parker, Baker, & Smith's model of the evolution of anisogamy (the PBS model) takes as its starting point that isogamous broadcast spawners where gametes are released in an aquatic environment and fertilization occurs by random encounters between gametes (Parker et al 1972). Under these circumstances, males who can produce more abundant and smaller sperm benefit from higher search efficiency and are more successful to fertilize eggs and therefore are favored (Parker et al. 1972; Lessells et al. 2009). This process through which gametes from different males compete for higher mating efficiency is called gametic competition and is assumed to be the major selective force in the evolution of tiny and numerous sperm in sexual eukaryotes (Lessells et al. 2009).

An alternative process that may influence the evolution of gamete size and number is "sperm limitation." In broadcast spawners, the chance that sexually compatible gametes (i.e. egg and sperm) meet to fuse and produce zygotes might be low, and therefore, some eggs may remain unfertilized (Lessells et al. 2009): a condition called sperm limitation. Researchers speculate that sperm limitation may select for faster motility, to increase the chance of finding the opposite gamete, or for larger target size (egg size), to increase the search and fusion efficiency (Lessells et al. 2009).

In this issue, Liao et al. investigated the relative importance of sperm competition and sperm limitation on the evolution of sperm size and number in anurans and fishes. Liao and colleagues conducted phylogenetic models and path analyses for the two taxa. They coupled these analyses with extensive measurements of ejaculate traits (number and size of sperm) and qualitative information of spawning conditions.

They found that ejaculate traits in anurans and fishes have evolved differently due to their different spawning conditions and reproductive biologies. Male anurans release sperm while in amplexus with the females, thus placing sperm very close to eggs. In some species, mating occurs in a nest-like environment, which further protects the gametes from dispersal. These types of behavior decrease the chance of gametes being dispersed by water currents, but intensify the selection force on the ability of sperm to effectively penetrate the gelatinous coating of eggs. Liao et al. conclude that sperm length and number in anurans were mainly characterized by variation in sperm competition, and therefore were strongly influenced by a size/number trade-off.

Liao et al. found that, in contrast to anurans, the evolution of ejaculate traits in fishes was more strongly influenced by egg number and water turbulence, which points to sperm limitation. This is because fish are broadcast spawners and release gametes in an aquatic environment where gametes are prone to dispersal due to water currents.

Liao and colleagues' finding that sperm limitation might be a more important factor in the evolution of sperm size and number in broadcast spawners contradicts the generally accepted models of evolution of anisogamy. Such models suggest sperm competition is a more robust factor in shaping the evolution of anisogamy originating from an isogamous broadcast spawner ancestor (Parker et al. 1972; Lessells et al. 2009). Moreover, conditions of spawning have never been considered in models of the evolution of anisogamy. In conclusion, Liao et al.'s findings are novel and compelling enough to provide more weight to sperm limitation as an important factor in the evolution of anisogamy when the ancestor was a broadcast spawner as described by Parker et al. (1972).

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