Sperm competition, sexual conflict, and speciation: a comment on Tinghitella et al.

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While Darwin’s theory of sexual selection via male contest competition was readily accepted as an evolutionary driving force, female choice was not. The initial rejection of female choice initiated over 100 years of theoretical and empirical research effort that has culminated in a rich appreciation of female choice as an engine of speciation. But as (Tinghitella et al. 2018) rightly highlight, the intense focus on female choice has been accompanied by a neglect of the role of male contest competition in the speciation process. Tinghitella et al. (2018) provide a timely overview of the various mechanisms by which sexual selection through male contest competition might generate phenotypic divergence among and within populations, and provide us with a research agenda with which to redress the balance in research effort on the evolutionary consequences of Darwin’s other mechanism of sexual selection. What Darwin did not appreciate was that sexual selection continues beyond mate acquisition, in the form of sperm competition and cryptic female choice (Simmons 2001). While Tinghitella et al.’s review focused on male competition prior to mating, it is important to highlight the evolutionary consequences of sperm competition for speciation, and its interplay with premating male contest competition.

When females mate with more than one male, sexual selection will favor adaptations in males that allow them to pre-empt the sperm stored by females from rival males and prevent females from accepting further matings that might result in the loss of paternity (Simmons 2001). For example, male intromittent genitalia can function in the removal of rival sperm during copulation such that males with genital morphology better equipped to remove rival sperm gain a selective advantage during fertilization. As noted by Tinghitella et al. (2018) populations can vary in operational sex ratio or density, both factors which are known to affect the risk and intensity of sperm competition and selection for male expenditure on sperm competition traits (Simmons 2001). Population divergence in male genital traits used in sperm competition with rivals can result in mechanical incompatibilities among populations when they come together, imposing reproductive isolation and speciation (e.g., Wojcieszek and Simmons 2013).

Male adaptations for sperm competition may not always be in the best interests of females. Male seminal fluid proteins can profoundly affect female reproductive physiology, promoting rapid egg deposition and/or inhibiting female sexual receptivity to rival males (Arnrqvist and Rowe 2005). In this way, seminal fluid proteins represent an important weapon in the arsenal of male postmating competition for fertilizations. In some species, seminal fluid proteins are absorbed through the female’s reproductive tract and into her bloodstream, while in others, the male’s genitalia can pierce the female’s reproductive tract allowing direct access of seminal fluid to her body cavity. Importantly, seminal fluids that benefit males in postmating sperm competition are frequently costly for females (Arnrqvist and Rowe 2005). Females can suffer energetic costs associated with reproductive tract wound repair, they can be exposed to pathogens during traumatic insemination, or seminal fluid proteins can reduce female mating frequency below that which is optimal for lifetime reproductive success. Seminal fluid proteins that promote male fitness can even be toxic, reducing female lifespan. Sexual selection via sperm competition is also known to favor increased numbers of sperm in the ejaculate, and sperm that have increased fertilization capacity (Simmons 2001). High densities of competitive sperm can be detrimental to female fitness when they result in polyspermy (Arnrqvist and Rowe 2005). Postmating sexual selection acting on males can thereby generate cycles of antagonistic coevolution between males and females that can drive extremely rapid evolutionary divergence and speciation, both in sympathy (Gavrilets and Waxman 2002) and allopatry (Gavrilets 2000). Indeed, comparative analyses have revealed greater species diversity among clades of insect with postmating sexual selection compared with clades where females mate only once (Arnrqvist et al. 2000).

Arnrqvist and Rowe (2005) suggest that postmating sexually antagonistic coevolution may be a more potent driver of speciation than other forms of intersexual selection because selection on females will be direct, via the costs of sperm competition traits in males, rather than indirect through the benefits required by models of female choice. Sperm competition may also be a more powerful driver of speciation than male contest competition. When females mate multiply, the strength of premating sexual selection acting on males will be greatly diluted (Parker and Birkhead 2013). A general understanding of the role of male competition in speciation may therefore encompass mechanisms of sexual selection operating before, during, and after mating.

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