



## Invited Commentaries

### The research bias is unfortunate but also unsurprising: a comment on Tinghitella et al.

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Sexual selection continues to be an active and exciting focus of research for behavioral ecologists and evolutionary biologists, but also continues to be heavily biased towards studies of female mate choice. In particular, research on sexual selection as a driver of speciation has focused almost exclusively on the role of mate choice. Tinghitella et al. (2018) offer a timely and insightful review that expands our understanding of how sexual selection can contribute to speciation. The authors summarize recent evidence that shows how male–male competition can facilitate divergence in sympatry, allopatry, and secondary contact, and give specific recommendations for future research.

Tinghitella et al. (2018) argue that our ability to describe how sexual selection contributes to speciation has been hampered by the fact that the potential impact of male–male competition has been largely overlooked. We believe that this oversight is due (at least in part) to imprecise terminology by sexual selection researchers—an issue that we argue has hampered our understanding of sexual selection in general (McCullough et al. 2016). For example, Tinghitella et al. highlight that previous authors have erroneously defined speciation by sexual selection as occurring when “a parallel change in mate preference and secondary sexual traits within a population leads to prezygotic isolation between populations” (Panhuis et al. 2001). This is a perfect example of the problem with conflating terms: when “sexual selection” is used synonymously with “mate preference” or “mate choice”, research on the other components of sexual selection get ignored (McCullough et al. 2016). We hope that the review by Tinghitella et al. (2018) not only encourages more research on the role of male–male competition in driving speciation, but also, and more broadly, that it reminds researchers that male–male competition and female choice are distinct mechanisms of sexual selection.

There is another reason why it is not surprising that research on speciation by sexual selection has focused more on the role of mate choice than male–male competition: the potential for mate choice to lead to assortative mating is simply more direct. Because females often select mates based on their preferences for secondary sexual traits, differences in female mate choice can be a direct barrier to gene flow between diverging populations. Although theoretical models suggest that mate choice is more likely to promote species divergence in conjunction with other processes (e.g., divergent ecological selection and/or divergent male–male competition), and probably rarely occurs on its own (van Doorn et al. 2004; van Doorn et al. 2009), there is still obvious intuitive appeal in the hypothesis that female preference can

be a powerful driver of speciation given the direct links between mate preference, mate selection, and reproductive isolation.

By contrast, male–male competition is expected to be less effective in promoting speciation because additional processes are almost certainly required to prevent homogenizing gene flow between diverging populations (van Doorn et al. 2009). Even if male–male competition contributes to the divergence of male phenotypes, unless females differ in their choice of breeding habitats, or unless they choose males on the basis of competitive phenotypes, then male–male competition may have little potential to strengthen assortative mating and the likelihood of speciation. That is, speciation by male–male competition may not depend on differences in female preference for secondary sexual traits, but without reinforcement from female choice, speciation by male–male competition probably would require some other form of divergent ecological selection. Intriguingly, comparative studies find support for the hypothesis that male–male competition has a weaker effect on speciation than mate choice: speciation rate is positively correlated with dichromatism, which is probably targeted by female choice, but negatively correlated with sexual size dimorphism, which is probably favored in the context of male–male competition (Kraaijeveld et al. 2011). We doubt that male–male competition is ever a stronger or faster driver of speciation than female choice. However, we agree with Tinghitella et al. that more empirical, theoretical, and comparative studies are clearly needed to determine when male–male competition *can* and *is most likely* to contribute to species divergence.

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## REFERENCES

- van Doorn GS, Dieckmann U, Weissing FJ, Associate Editor: Sergey Gavrilets. 2004. Sympatric speciation by sexual selection: a critical reevaluation. *Am Nat.* 163:709–725.
- van Doorn GS, Edelaar P, Weissing FJ. 2009. On the origin of species by natural and sexual selection. *Science.* 326:1704–1707.
- Kraaijeveld K, Kraaijeveld-Smit FJ, Maan ME. 2011. Sexual selection and speciation: the comparative evidence revisited. *Biol Rev Camb Philos Soc.* 86:367–377.
- McCullough EL, Miller CW, Emlen DJ. 2016. Why sexually selected weapons are not ornaments. *Trends Ecol Evol.* 31:742–751.
- Panhuis TM, Butlin R, Zuk M, Tregenza T. 2001. Sexual selection and speciation. *Trends Ecol Evol.* 16:364–371.
- Tinghitella RM, Lackey ACR, Martin M, Dijkstra PD, Drury JP, Heathcote R, Keagy J, Scordato ESC, Tyers AM. 2018. On the role of male competition in speciation: a review and research agenda. *Behav Ecol.* 29:783–797.