selection. A recent study reports divergent selection gradients from male competition substantially stronger than many reported ecological selection gradients (Keagy et al. 2016). However, male competition has not been front and center in work on sexual selection and speciation, despite being a ubiquitous source of strong selection and an arbiter of mating success. This review is timely given several compelling recent papers and mounting evidence. The authors do a nice job covering the importance of geographic context and summarize some key ideas that have been explored, while pointing out fruitful avenues for future work. Here I highlight some additional ideas of when male competition can alter the speciation process.

Male competition can have direct effects, but also can modify the effects of mate choice and ecology on speciation. It can either increase or decrease reproductive isolation, or make isolating barriers "leaky" depending on how it interacts with both mate choice and ecological factors. These interactions can be complex. For example, male competition has fostered divergence as reproductive isolation accumulated, but also contributed to the reversal of this process as species fused (Keagy et al. 2016). In another example, the red backed fairy wren mating system is rife with extra pair copulations, and females of both red and orange subspecies choose red males as extra pair mates. Female choice undermines isolation in an asymmetric manner, whereas male competition for territories and mates maintains isolation (Greig et al. 2015). Thus, the two forms of sexual selection combine to allow introgression of red plumage onto the orange genomic background. In this system, male competition enhances isolation, whereas in wall lizards where female choice is weak, male competition causes introgression and depletes reproductive isolation (While et al. 2015). How do we know when male competition helps versus hinders speciation?

Not only can we advance by considering both aspects of sexual selection, but also by considering mate choice by both sexes. Males can be choosy, and some theory considers how male competition alters the evolution of male mate choice, which in turn may affect speciation. Typically, male competition limits the evolution of male choice because choosy males compete more for access to preferred females. However, male competition can enhance isolation when choosy males allocate courtship effort strategically in a competitive context, which in turn can create substantial linkage disequilibrium and in some conditions lead to nearly complete assortative mating (Rowell and Servedio 2009). I encourage more theoretical and empirical work considering how male competition affects both female and male choice of mates, and when this enhances or undermines reproductive isolation.

Disruptive selection can lead to divergence and reproductive isolation, and the review summarizes some current theory of male competition's role, which mostly focuses on the effects of frequency-dependent selection. However, frequency-dependent selection has not always been seen when male competition contributes to speciation (Keagy et al. 2016). Moreover, because speciation requires both divergence and reproductive isolation, it is less likely than alternative outcomes such as polymorphism or plasticity (Rueffler et al. 2006). Indeed, intense male competition is a primary cause of alternative mating strategies—polymorphisms in male competitive traits that do not typically cause reproductive isolation. Both theoretical and empirical work to understand when polymorphism versus speciation is likely given ecological and social conditions could bear fruit.

One way to make progress may be by emphasizing the relationship between competition for resources (ecological competition) and competition for mates (male competition). The rich body of theoretical and empirical work on ecological competition, niche evolution, and ecological speciation could be leveraged to move our understanding of male competition in speciation forward. Substantial progress has been made adapting ecological principles to study how individual behavioral variation affects reproductive isolation (Bolnick et al. 2003; Boughman and Svanbäck 2017) so this suggestion follows in that tradition. In ecological speciation, resource competition generates disruptive selection generating both premating and ecologically dependent postmating isolation. Although the review restricts itself to premating effects, male competition often continues after mating via sperm or pollen competition also interacting with cryptic female choice, and these dynamic processes can cause substantial prezygotic and postzygotic isolation (Martin and Hosken 2003). There is much intriguing work to be done on the full spectrum of effects male competition can have on the speciation process.

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A major player need not be the only player in speciation: a response to comments on Tinghitella et al.

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We are delighted that our recent review (Tinghitella et al. 2018) has garnered broad interest and thoughtful commentary. Collectively, it is clear that the link between competition for mates and divergence in competitive phenotypes is well supported. As we and the invited commentary authors point out, it is less clear when mate competition can and is most likely to cause reproductive isolation. Here, we wish to highlight some solutions offered by the Invited Commentaries, and to reiterate that while competition for mates might not act alone to cause speciation, ignoring it altogether will leave gaps in our understanding because mate competition may initiate, enhance, stabilize, or hinder divergence. After all, ecological speciation requires assortative mating, and sexual selection via mate choice is less likely to cause speciation in the absence of ecological divergence.

What is the range of scenarios under which competition for mates can contribute to reproductive isolation? As McCullough and Emlen (2018) point out, the unclear relationship between male competition and reproductive isolation is largely responsible for the absence of male competition in the speciation literature. Simmons (2018) helps to fill this gap by considering postcopulatory sperm competition and the potential for sexual conflict. These coupled processes can result in divergence between lineages in genital morphology and male–female postcopulatory molecular interactions, generating rapid evolution of reproductive isolation.

It is more difficult to determine how precopulatory male competition could result in reproductive isolation. The best studied mechanism is negative frequency-dependent selection of competitive phenotypes, which can generate distinct morphs and favor assortative mating via selection against hybrids and reinforcement (Dijkstra and Border 2018). Burdfield-Steel and Shuker (2018) emphasize the centrality of reproductive isolation to speciation and offer that females must be the ultimate arbiters of isolation. We agree that speciation by male competition would be most likely under circumstances that link mate choice to competitive traits. But, females need not be the choosy sex. Recent work suggests a dual role for males in speciation as both competitors and choosers (Boughman 2018; Tinghitella et al. 2018). Male darter fish, for instance, compete for access to females and display divergent male color patterns that have coevolved with competitive responses. Yet, male darters are also the choosier sex in an interspecific context (Mendelson et al. 2018). So, though male–female interactions are likely integral to speciation by male competition, it may be more accurate to assume the need for competitors and choosers, whether or not these roles are filled by 1 or 2 sexes.

Lehtonen (2018) and Simmons (2018) call for embedding our understanding of the role of competition for mates in the context of different mating systems because the strength and nature of selection on competitors' traits should depend on the opportunity to monopolize mates. In polygynous or polyandrous mating systems, the potential to monopolize mates is high and, thus, intrasexual competition significantly affects mating success. Strong male competition is most likely in polygynous systems, and pre and postcopulatory sexual selection resulting from this competition should be greater in systems with more male-biased operational sex ratios. Although polyandry is expected to decrease the strength of male competition (Simmons 2018), it should increase the strength of female competition, which can also contribute to divergence and speciation (Lipshutz 2018). Importantly, in systems where males and females have multiple mates, both male and female intrasexual selection can occur. Intrasexual competition in both sexes could facilitate speciation via frequency-dependent intrasexual selection and mate choice (van Doorn et al. 2004) or via sexual conflict (Simmons 2018). Lehtonen (2018) pushes further, blurring the lines between ecological and sexual competition (Boughman 2018; Dijkstra and Border 2018), to discuss how competition among socially monogamous mated pairs (instead of individuals) for resources could lead to speciation.

In summary, we advocate a holistic approach to speciation research that carefully considers the biology of the study system and the processes likely to be at play. Such an approach should include broad thinking about interacting mechanisms and sex-specific mating strategies, and thoughtful consideration of both pre and postcopulatory mate competition. Speciation is perhaps the greatest show on Earth, but we have not been paying attention to all the players driving this performance. When we do, our appreciation and understanding will be that much more complete.

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