

Editorial

Male competition and speciation: expanding our framework for speciation by sexual selection

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Introduction

Sexual selection is a powerful source of rapid evolutionary change, and there is a long-standing hypothesis that it can cause reproductive isolation. However, our understanding of speciation by sexual selection is largely limited to mechanisms by which sexual selection via female mate choice can drive divergence (i.e., when male mating signals and female preferences for those signals diversify; Panhuis et al. 2001; Maan and Seehausen 2011). Male competition for mates—Darwin's second mechanism of sexual selection—can also favor rapid and dramatic phenotypic and genotypic changes, yet it has been all but overlooked in speciation research (Darwin 1859, 1871; Seehausen and Schluter 2004; Qvarnström et al. 2012; Tinghitella et al. forthcoming).

Evidence suggests that male competition is capable of driving divergence and potentially contributing to the speciation process. First, male competition can generate strong selection that favors divergent phenotypes within and between populations. In some mating systems, male competition primarily determines mating success within populations (e.g., resource or harem defense polygyny; West-Eberhard 1983; Andersson 1994). In other mating systems, male competition acts as a filter, determining which males have access to females and, thus, the phenotypes available for female mate choice (Wong and Candolin 2005; Hunt et al. 2009). Further, the remarkable diversity in competitive phenotypes (i.e., weapons, agonistic signals, and competitive strategies; Seehausen and Schluter 2004; Grether et al. 2013; McCullough et al. 2014) likely results from population differences in selection generated by competition for mates. Second, it is well established that competition for resources can drive speciation via natural selection (Schluter 2001; Pfennig and Pfennig 2010). Competition for mating resources could have similar potential to shape the speciation process.

This special column addresses how and when competition for mates can generate and maintain divergent phenotypes and facilitate reproductive isolation. Moreover, the contributed papers consider how competition for mates might hinder divergence and speciation. Our aims are to expand our current speciation framework to include

the contribution of male competition, explore the diversity of mechanisms by which male competition drives divergence, and motivate future work by identifying key questions and gaps in our current understanding. Whereas most work in this emerging field has focused on male–male competition, female–female competition may be similarly capable of driving divergence and speciation. Female–female competition can arise when males are a limiting resource, including, but not limited to, sex-role-reversed mating systems. Within-sex competition for mates among males or females can generate disruptive, frequency-dependent selection of mate preferences and facilitate divergence and speciation (van Doorn et al. 2004). Thus, the ideas discussed throughout this column apply broadly to within-sex competition for mates.

Key Questions in the Study of Competition for Mates and Speciation

Recent work sheds light on how and when competition for mates likely affects speciation (Seehausen and Schluter 2004; Dijkstra and Groothuis 2011; Qvarnström et al. 2012; Tinghitella et al. forthcoming). One critical challenge has been to determine whether and how divergence favored by competition for mates could contribute to reproductive isolation. We briefly review recent findings organized by 3 key questions. We then describe the contributions in the special column that address each of these questions.

How does competition for mates contribute to divergence and speciation in different geographic contexts?

In sympatry, the best-studied mechanism of divergence and speciation via competition for mates is negative frequency-dependent selection, which could allow a novel competitive phenotype to invade a population and stabilize the presence of multiple morphs (Mikami et al. 2004; Seehausen and Schluter 2004; van Doorn et al. 2004). In this scenario, males bias aggression to similar phenotypes because, for example, they compete for shared resources. Thus,

males with a rare phenotype experience a fitness advantage because they receive relatively little aggression (Seehausen and Schluter 2004; van Doorn et al. 2004). Furthermore, selection could favor females who choose males with a rare phenotype because, for example, these males may have more energy to invest in mate provisioning or paternal care. Competition for mates may also favor divergent competitive phenotypes independent of their frequency because alternative fitness optima exist (Lackey and Boughman 2013; Keagy et al. 2016). In this case, males with phenotypes intermediate to existing fitness optima would be selected against in competition. Moreover, selection against mating between types could favor the evolution of prezygotic isolation via reinforcement (Servedio and Noor 2003). In allopatry, competitive phenotypes could diverge due to environmental differences (e.g., Scordato 2017) or via the accumulation of different alleles in populations adapting to similar environments (i.e., mutation order divergence; Martin and Mendelson 2012; Mendelson et al. 2014). Ecological conditions that likely shape divergence in competitive phenotypes include differences in signaling environments, presence of predators or parasites, availability of prey, and habitat structure (e.g., Maan and Cummings 2012; Qvarnström et al. 2012; McCullough et al. 2016; Scordato 2017; Tinghitella et al. forthcoming). If competitive phenotypes are locally adapted, then divergent natural selection between populations from different environments could facilitate habitat isolation, and divergent sexual selection from mate preferences for locally adapted traits could result in sexual isolation. In secondary contact, the likelihood of divergence between previously isolated populations depends largely on the extent to which competitors share mating resources. When competitors from different populations do not compete for access to the same mates, competitive phenotypes are expected to diverge to reduce costly agonistic interactions with noncompetitors (i.e., agonistic character displacement, Grether et al. 2009; Grether et al. 2013). In contrast, shared resources among interspecific competitors favors *convergence* of agonistic traits (Grether et al. 2009, 2013; Drury et al. 2015).

How do natural selection, mate choice, and competition for mates interact to affect the potential for speciation?

Work on the contribution of female mate choice to speciation suggests that sexual selection is most likely to cause speciation when acting in concert with natural selection, rather than when acting alone (van Doorn et al. 2004; Ritchie 2007; Servedio and Boughman 2017). Competition for mates may also facilitate divergence and speciation, most often through interactions with natural selection and/or mate choice. Numerous examples demonstrate that environmental dependence of competitive phenotypes could affect divergence (e.g., Vallin and Qvarnström 2011; Lackey and Boughman 2013; Heathcote et al. 2016; McCullough et al. 2016). Divergence and speciation in 2 well-studied examples of rapid speciation (i.e., cichlid fish, limnetic-benthic stickleback fish) involve interactions between divergent ecology, female mate choice, and male competition (Schluter 1993, 1995; Boughman 2001; Seehausen and Schluter 2004; Seehausen et al. 2008; Lackey and Boughman 2013). Yet, recent work in European wall lizards reveals that male competition and ecology can shape divergence and reproductive isolation in the absence of female mate choice (Heathcote et al. 2016). Interactions among sources of selection could also hinder speciation. For instance, sexual selection from competition for mates should limit trait divergence when selection on competitive phenotypes conflicts with divergent natural selection (see Servedio and Boughman (2017) for parallel ideas for female preferences).

How do aggression biases and competitive asymmetries arise and affect divergence?

Competitors may bias aggression toward particular phenotypes (e.g., homotypic, heterotypic, or a certain trait value regardless of species or population; Pauers et al. 2008; Dijkstra and Groothuis 2011; Lehtonen 2014; Lehtonen et al. 2015). In sympatry, an aggression bias for homotypics could evolve early in divergence if there is pleiotropy or tight linkage between the competitive phenotype and aggression, when aggression is learned and targeted toward the most common phenotype encountered, or via imprinting (Seehausen and Schluter 2004; Dijkstra and Groothuis 2011). In secondary contact, selection against competition with heterospecifics that do not share mating resources could favor the evolution of conspecific aggression bias (Grether et al. 2009; Anderson and Grether 2010). Aggression biases toward homotypics generate negative frequency-dependent selection that can allow a novel competitive trait to invade the population and facilitate initial divergence in sympatry. Aggression biases for homotypics can also stabilize coexistence of closely related species with different competitive phenotypes (Seehausen and Schluter 2004; Dijkstra et al. 2007; Pauers et al. 2008; Lehtonen 2014).

Aggression biases and competitive ability may differ between morphs with important consequences for maintaining divergent competitive phenotypes. An asymmetric aggression bias occurs when 1 morph biases aggression to homotypics, for example, while the other morph does not bias aggression and competes equally with both morphs. Competitive asymmetry can occur when 1 morph has an advantage at winning contests over the other morph, and competitive asymmetries appear to be very common (Martin et al. 2017). Asymmetries in aggression bias and competitive ability could arise, for example, in allopatry due to differences in selective environments (e.g., signaling contexts, resource density, predators) or via mutation order divergence (Qvarnström et al. 2012; Tinghitella et al. forthcoming). An asymmetry between morphs in aggression bias could lead to competitive exclusion of the morph that receives more aggression (i.e., receives both homo- and heterotypic aggression), although habitat or resource partitioning between morphs could facilitate coexistence (Dijkstra et al. 2007; Dijkstra and Groothuis 2011; Lehtonen et al. 2015). A competitive asymmetry in which a novel morph has a competitive advantage would allow the novel morph to invade a population, which could facilitate early divergence between morphs in sympatry (Dijkstra et al. 2005). Competitive asymmetries between species in secondary contact could result in competitive exclusion and potentially facilitate habitat isolation (Owen-Ashley and Butler 2004; Duckworth 2006; Vallin et al. 2012; Lipshutz 2017). Alternatively, competitive asymmetries could homogenize populations through asymmetric introgression (While et al. 2015). The latter scenario may be more likely with strong competitive asymmetries and weak divergent selection from other sources.

Contributions to This Issue

In this column, the 2 review papers and 4 empirical papers each address the key questions described above. Importantly, these articles expand our framework for the role of speciation by sexual selection by examining a variety of mechanisms through which competition for mates could contribute to divergence and speciation.

The review by Lipshutz (2018) broadens our understanding of how within-sex competition might drive divergence and contribute to speciation by reviewing a growing body of literature on species

interactions in secondary contact and hybridization. The review offers a fresh perspective on sexual selection and hybridization, pinpointing how the outdated dichotomy between choosy females and competitive, but non-choosy, males oversimplifies sex roles and limits our perspective on mechanisms that might contribute to speciation. Lipshutz (2018) considers how female–female competition, interactions between female choice and male competition, and character shifts in competitive traits and recognition can facilitate or impede reproductive isolation. Female–female competition might be particularly relevant when the fitness costs of mating with heterospecifics are low for females. Several mechanisms by which interspecific within-sex competition might promote reproductive isolation are outlined, including some that involve interactions with mate choice (e.g., reproductive and agonistic character displacement) and some that do not (e.g., competitive asymmetry and reproductive exclusion). Finally, the flip-side of interactions in secondary contact is considered: when do interspecific interactions promote, rather than reduce, hybridization? Lipshutz (2018) reviews evidence that competitive asymmetry can promote directional hybridization between species that still share mating resources, generating sometimes asymmetric introgression of loci from the competitively superior parental type to the competitively inferior type. Our understanding of how within-sex competition facilitates hybridization is in its infancy, and female–female competition is understudied relative to male–male competition, making this area ripe for future work.

Dijkstra and Border (2018) review multiple mechanisms through which male competition can cause divergence of competitive phenotypes and contribute to reproductive isolation. Although negative frequency-dependent selection has been the primary explanation of speciation in sympatry, Dijkstra and Border (2018) extend this hypothesis to the contexts of allopatry and secondary contact. The authors describe how aggression biases toward homotypic males as well as a competitive advantage of the novel phenotype could yield negative frequency-dependent selection and disruptive selection, which can both facilitate the invasion of a novel phenotype and promote coexistence of 2 morphs (Seehausen and Schluter 2004; Dijkstra and Groothuis 2011). Furthermore, the authors discuss how competitive traits likely result in trade-offs with other traits, such as physiological or life history traits. Given these trade-offs, different competitive phenotypes may be adaptive alternatives, with each phenotype maximizing a different end of the trait distribution. For instance, if investing in color limits energy available for growth, then alternative competitive phenotypes may be colorful and small versus dull and large. Moreover, the authors draw parallels between how ecological competition and male competition contribute to speciation. Considering these 2 mechanisms simultaneously provides a framework for understanding how natural and sexual selection interact during divergence.

Moran and Fuller (2018) step outside the traditional dyadic model of comparative speciation studies to ask whether sympatric interactions among congeners can facilitate divergence in competitive phenotypes across an allopatric radiation of closely related fish species. Darters are a diverse group of fish that often exhibit striking, species-specific male nuptial color patterns and drably colored females. The rainbow darter *Etheostoma caeruleum* is widely distributed in rivers and streams of the Eastern United States and co-occurs with several members of the orangethroat darter species group throughout the entirety of their ranges. Other species in the orangethroat darter group are either partially or completely allopatric with respect to the rainbow darter. In staged contests, only

males of multiple orangethroat darter species from populations sympatric with the rainbow darter biased aggression toward conspecifics, whereas males from populations allopatric to the rainbow darter showed no aggression bias. Similarly, males only biased their courting efforts toward conspecific females when males were from a population sympatric with the rainbow darter. Thus, Moran and Fuller (2018) find evidence consistent with male-driven agonistic and reproductive character displacement. Female mate choice appears unimportant as no species exhibited a significant conspecific bias. In addition, the authors find evidence consistent with cascade agonistic and reproductive character displacement. In staged encounters between 2 allopatric species of orangethroat darter, only males from populations sympatric with rainbow darters bias aggression to conspecifics and choose conspecific mates. These findings suggest that sympatric interactions between orangethroat darter species and the rainbow darter may strengthen reproductive isolation between closely related, allopatric orangethroat darter species as a byproduct. The patterns described by Moran and Fuller (2018) motivate future work to test the roles of both inter- and intraspecific competition for mates in speciation.

Tinghitella et al. (2018) advocate for placing our understanding of heterotypic aggression biases and competitive asymmetries in a sexual signaling context because competitive outcomes may depend on how receivers perceive and respond to signals. The authors staged competition trials over a single nesting site within and between color morphs (red or black) of threespine sticklebacks *Gasterosteus aculeatus* from Washington state (United States) and assessed the relationships between competitive outcomes and putatively sexually selected colors and behaviors. Tinghitella et al. (2018) find a complex interaction between the traits that predict competitive success within and between male color types, demonstrating that males of the 2 color types use different competition “currencies.” Regardless of competitor type, red and black males who successfully established territories performed more aggressive behaviors than losing males. However, color predicted competitive outcomes differently for red and black males. Red males with more extensive red color were more likely to win territorial disputes with homotypic males, but less likely to win against heterotypic males. Thus, whether the extent of color serves as a signal of aggressive behavior depends on the receiver. In black males, however, the extent of black color does not predict competitive outcomes; only aggressive behaviors were associated with winning in territorial disputes. In summary, divergent competitive strategies may explain the aggression biases and asymmetries that are frequently observed upon secondary contact. Tinghitella et al. (2018) describe how asymmetries in competitive abilities could facilitate spatial segregation, reinforcing reproductive isolation.

Bierbach et al. (2018) investigate how abiotic environments shape fighting ability and, thus, the outcomes of competition between ecotypes at the interface between habitats. The authors investigate competitive outcomes between populations of poeciliid fish that are locally adapted to toxic, hydrogen sulfide-rich environments and those from non-sulfidic aquatic environments. The authors suggest *a priori* that physiological and metabolic adaptation to extreme environments could incur costs that limit energy investment in male competition and in reproductive interactions more generally. Two major results consistent with this hypothesis emerged: 1) extremophile males from 1 drainage, but not all drainages investigated, exhibit lower aggression levels than males from non-sulfidic environments, and 2) in pairings between ecotypes, non-sulfide-adapted ecotypes were more likely to win contests when

fighters were staged in non-sulfidic environments. Importantly, not all extremophile males suffer the proposed costs of adaptation to extreme environments. Rather, the authors argue that adapting to hydrogen sulfide-rich environments limits resource holding potential when competing with males from non-sulfidic environments. This competitive asymmetry could contribute to reproductive isolation by reducing gene flow when extremophile males migrate into more benign habitats because they lose fights against males who are locally adapted to those habitats.

Becher and Gumm (2018) investigate whether male competition and female mate choice are likely to facilitate coexistence upon secondary contact between endemic and recently introduced populations in the same genus: the endemic Red River pupfish *Cyprinodon rubrofluviatilis* and the introduced sheepshead minnow *Cyprinodon variegatus*. In interspecific dominance trials, males of each species won an equal number of fights. However, males of the endemic species used a greater number of aggressive behaviors to gain dominance than males of the introduced species. Males that invest energy in male competition may have limited energy to maintain a territory or court females. Thus, endemic males may have reduced mating success. Moreover, the competitive asymmetry between endemic and introduced males could reduce the likelihood of coexistence and lead to local extinction of the endemic species. Females of both species lacked consistent preferences at the population level; some individual females of each species strongly preferred conspecifics, some strongly preferred heterospecifics, and others had no preference. Population-level preferences were equivalent to random mating and, therefore, would not limit hybridization between the species. Thus, male competition may be more important than female mate choice for determining the likelihood of hybridization upon secondary contact.

In combination, the articles in this special column expand our understanding of how and when competition for mates contributes to divergence and speciation. The contributed papers highlight several ways that competition for mates can affect divergence and the potential for reproductive isolation, many of which emphasize the role of divergent natural selection and some of which involve little to no role for female mate choice. Future theoretical work will be particularly well suited to determine whether competition for mates alone can lead to speciation or whether other diversifying forces (e.g., natural selection, female mate choice, male mate choice, or female–female competition) are required (van Doorn et al. 2004). Previous experimental and theoretical studies have often measured outcomes of competition for mates and predicted potential divergence using population means. However, findings from this special column motivate future work to examine variation among individuals in competitive phenotypes and responses; the nature of this variation could affect the speed and likelihood of speciation as well as the maintenance of distinct species on secondary contact. Finally, this column highlights the importance of understanding how competition for mates may hinder divergence and speciation as a complement to understanding when competition promotes these processes. This special column serves as an exciting stimulus for future work on the role of competition for mates in speciation.

Acknowledgments

We would like to first thank Zhiyun Jia, the Executive Editor of *Current Zoology*, for the invitation to serve as guest editors as well as for his advice and help throughout. We have greatly enjoyed this opportunity to contribute to this emerging field. We are grateful for the authors who contributed their

work to this special column and to the reviewers who critically evaluated the work. Thanks to Tamra Mendelson and Maria Servedio for the thoughtful feedback that improved this manuscript.

Funding

The invitation to guest edit this special column resulted from a symposium co-organized by ACRL, MDM, and RMT at the 2016 congress of the International Society for Behavioral Ecology, and travel expenses for all authors were supported in part by the National Science Foundation (IOS-1637252). While guest editing this special column, ACRL was supported by NSF (DEB-1638997) and the Watershed Studies Institute at Murray State University. RMT was supported by NSF (IOS-1601531) and the University of Denver's Office of the Associate Provost of Research.

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