



Invited Review

On the role of male competition in speciation: a review and research agenda

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Support for the role of sexual selection in speciation has grown over the last 30 years. Work in this area, however, has largely focused on a single dominant question: when and how do divergent male sexual signals and corresponding female preferences lead to reproductive isolation? The field has not given adequate attention to the role that male competition, Darwin's second mechanism of sexual selection, might also play in speciation. In this review, we summarize recent work that shows precopulatory male competition can initiate speciation in sympatry, drive divergence of competitive phenotypes in allopatry, and strengthen reproductive barriers between competitive types during secondary contact. The manner by which male competition contributes to divergence in allopatry is a poorly understood yet compelling area of research; similar to female choice, male competition may be more likely to lead to speciation when working in concert with divergent ecology, and allopatry sets the stage for divergence among environments with reduced gene flow. To encourage future research in this area, we place potential mechanisms for speciation by male competition into existing speciation frameworks and propose a theoretical and empirical research agenda to reveal how male competition contributes to the accumulation of reproductive isolation. Our current understanding of when and how divergence in competitive phenotypes leads to reproductive isolation is limited, and theoretical work may be particularly well-suited to reveal when divergence by male competition is fastest and most likely.

Key words: agonistic character displacement, male competition, negative frequency-dependent selection, divergence, speciation.

INTRODUCTION

Speciation has been a focus in evolutionary biology since the field's inception, dating back to Darwin's *On the Origin of Species* (1859). Initial ideas about the "puzzle" of how species arise emphasized the

roles of geography and restricted gene flow: geographically isolated populations experience reduced gene flow and diverge as a result (Mayr 1963; Bush 1975). More contemporary efforts to understand speciation have expanded earlier conceptions to include a diversity of evolutionary mechanisms explaining genetic divergence and the generation of reproductive isolation (Panhuis et al. 2001; Schluter 2001; Turelli et al. 2001; Via 2001; Langerhans and Riesch 2013; Safran et al. 2013; Mendelson et al. 2014; Servedio 2016).

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The best-supported mechanism of speciation is ecological speciation, whereby divergent natural selection leads to trait divergence and subsequent reproductive isolation (Nosil 2012). Ecological speciation has received substantial support (Schluter 2001; Rundle and Nosil 2005; Nosil 2012; but see Hendry 2009). However, ecological speciation theory does not fully account for divergence of populations inhabiting similar environments, or divergence in systems in which exaggerated secondary sexual characters are the primary or only traits differing between closely related species, yet both scenarios characterize some particularly speciose animal groups (e.g., birds of paradise, Irestedt et al. 2009; cichlid fish, Turner et al. 2001, Salzburger et al. 2005; Hawaiian fruit flies, Kaneshiro 1988). Considering speciation mechanisms beyond ecological speciation, like sexual selection, founder-effect, and mutation order speciation, has provided a modern conceptual framework that differentiates the nature of selection (i.e., divergent vs. similar vs. reinforcing; Langerhans and Riesch 2013) and the distinct roles of ecological selection, sexual selection, and drift (Streelman and Danley 2003; Schluter 2009; Langerhans and Riesch 2013; Safran et al. 2013; Mendelson et al. 2014).

While the potential for sexual selection alone to drive speciation has been more controversial than the role of natural selection, it has nearly as long a history of study (Ritchie 2007). Sexual selection arises from within-sex competition for mates or gametes, where individuals of one sex, often males, compete directly through contests and/or indirectly through mate choice by the opposite sex (Andersson 1994). Darwin (1859; 1871) initially distinguished natural from sexual selection, but left the role of sexual selection in speciation as an implicit suggestion. Fisher (1930) provided the first verbal model of speciation by sexual selection via the coevolution of female mating preferences and male secondary sexual traits in divergent populations. This idea was later formalized with 2-locus (O'Donald 1980) and polygenic (Lande 1981) theoretical models, revitalizing interest in speciation by sexual selection (West-Eberhard 1983; Panhuis et al. 2001; Ritchie 2007). Empirical data have shown that sexual selection via female choice can act alone to drive the evolution of male secondary sexual characteristics (Mendelson and Shaw 2002; Grace and Shaw 2011), and that the extent of divergence in female preferences between lineages seems to best predict the likelihood of speciation (Rodríguez et al. 2013). However, many examples of sexual selection driving speciation involve synergistic ecological selection, which emphasizes the importance of interactions between sexual and natural selection (Ritchie 2007; Maan and Seehausen 2011; Scordato et al. 2014; Servedio and Boughman 2017).

Darwin and his contemporaries had little trouble reasoning that competition for mates could result in adaptations like exaggerated weaponry that enhanced mating success, but had more difficulty imagining how mating preferences could lead to differential mating success (Simmons 2001). Despite early dismissal of female preferences, over the past 25 years, more than 4 times as many papers have been published on female mate choice than male competition in leading behavior journals (McCullough et al. 2016). Similarly, research on speciation by sexual selection has largely ignored male competition (Seehausen and Schluter 2004; Qvarnström et al. 2012). Speciation by sexual selection has even been defined as occurring when “parallel change in mate preference and secondary sexual traits within a population” leads to prezygotic isolation between populations (Panhuis et al. 2001). Here, we argue that our ability to describe how sexual selection contributes to speciation has been hampered by overlooking male competition.

Compelling evidence that male competition is a potent evolutionary force capable of driving divergence comes from 3 major sources. First, in some mating systems, variance in reproductive success is determined primarily by male competitive interactions, with little influence of female mate choice (i.e., harem defense or resource defense polygyny in animals like deer, lizards, and horned beetles; West-Eberhard 1979; Clutton-Brock et al. 1982; Olsson and Madsen 1995; Emlen 1996). Further, the diversity of competitive phenotypes (i.e., weapons, agonistic signals, and competitive strategies) across taxa is consistent with male competition facilitating divergence (Andersson 1994; Emlen 1996; Simmons 2001; Taborsky 2001). Second, similarities between competition for ecological resources, an important driver of phenotypic divergence and speciation (Polechová and Barton 2005; Schluter 2009; Pfennig and Pfennig 2010), and male competition for mates suggest a potential role for the latter in speciation. Third, recent theoretical advances and empirical evidence more directly support a role for male competition in speciation in sympatry, allopatry, and secondary contact (Figure 1; Table 1).

In this review, we 1) consider existing evidence for how precopulatory male competition contributes to divergence in different geographic scenarios, 2) examine how male competition may interact with ecology and female mate choice, leading to speciation, and 3) articulate future research priorities. The speciation process involves divergence in traits (e.g., weapons, body size, behavioral strategies) and the underlying genes that may ultimately mediate the evolution of reproductive isolation. Most work to date on speciation by male competition focuses on trait divergence, and thus, our review will focus largely on this critical first step in the speciation process (but see Future Research Priorities). We use the terms “male competition” and “female mate choice” to reflect sex-specific roles represented in the majority of existing work, but note examples of female-female competition and male mate choice throughout. Importantly, the processes and predictions we describe apply broadly to “competitors” and “choosers” regardless of sex (akin to inclusive language for “signalers” and “choosers” in Rosenthal 2017). We focus here on precopulatory male aggression in animals. We recognize that sperm and pollen competition, both within and between populations, may rapidly generate incompatibilities that limit gene flow (Howard 1999; Manier et al. 2013; Baack et al. 2015), but these topics are beyond the scope of this review.

THEORETICAL AND EMPIRICAL EVIDENCE FOR THE ROLE OF MALE COMPETITION IN SPECIATION

Much work to date on the role of male competition in speciation has focused on adaptive speciation mechanisms in sympatry. In this section, and in Table 1 and Figure 2, we take a broader view to 1) describe and illustrate multiple nonmutually exclusive mechanisms by which male competition might contribute to speciation in sympatry, allopatry, and secondary contact, 2) link these hypothesized mechanisms to established speciation frameworks (Maan and Seehausen 2011; Langerhans and Riesch 2013, Safran et al. 2013, Mendelson et al. 2014), 3) identify key testable predictions deriving from these hypotheses, and 4) consider how mechanisms of male competition might interact with ecology and female mate choice. Although we discuss sympatric, allopatric, and secondary contact separately, several male competition mechanisms are relevant in all 3 scenarios (Table 1).

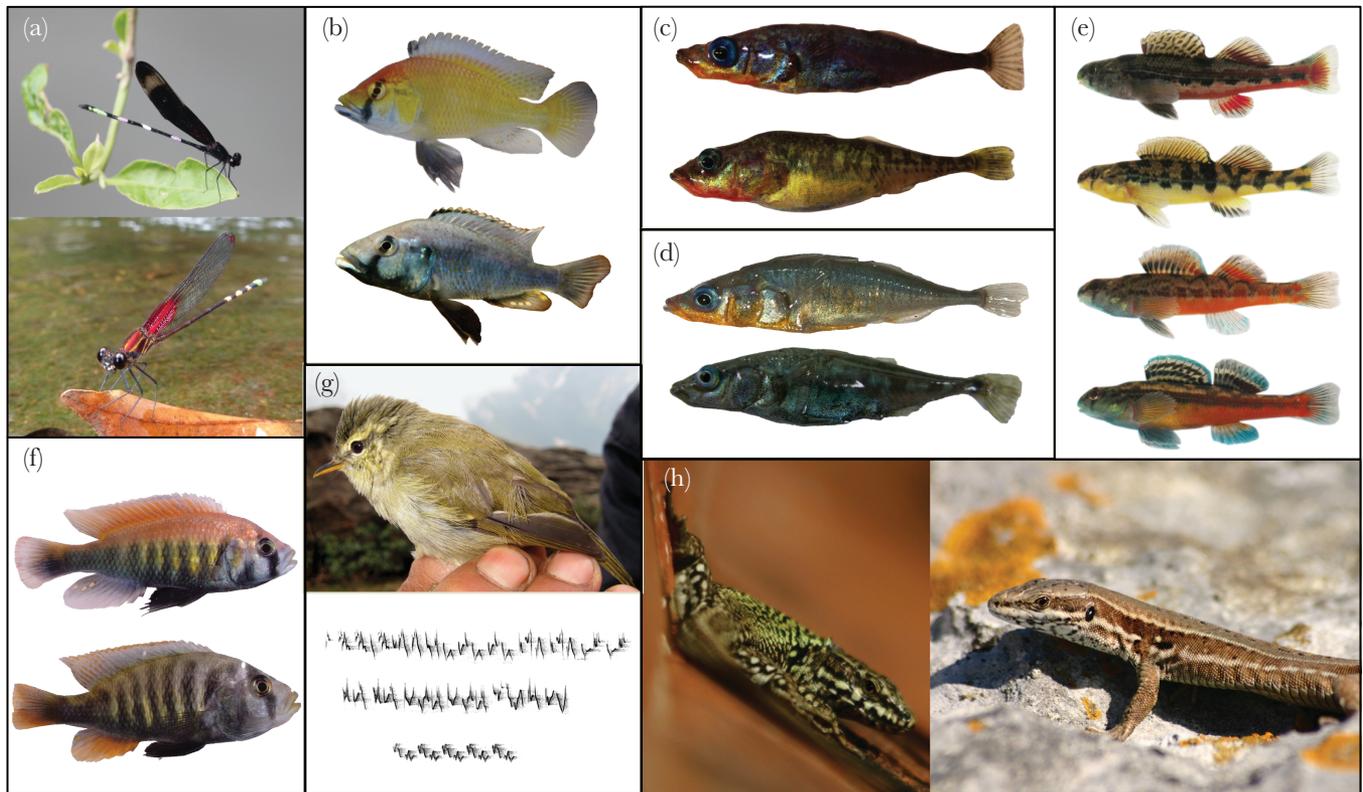


Figure 1

Example systems in which male competition is hypothesized to contribute to speciation. Empirical data support a role for male competition in divergence in at least a handful of systems including, but not limited to: (a) rubyspot damselflies (top: *Hetaerina titia*, bottom: *Hetaerina occisa*; photo credits: P. Green and J.P. Drury, respectively); (b) ecologically divergent Lake Massoko cichlid fish ecomorphs (photo credit: A. Tyers); (c) British Columbian 3-spine sticklebacks, *Gasterosteus aculeatus* (top: limnetic, bottom: benthic; photo credit: A. Lackey); (d) red and black 3-spine sticklebacks (top: red morph, bottom: black morph; photo credit: R. Tinghitella); (e) darter species pairs (from top to bottom: *Ethostoma etneiri*-*E. flavum* and *E. raneyi*-*E. zonistium*; photo credit: M. Martin); (f) Kissenda Island cichlid fish (top: *Pundamilia nyererei*, bottom: *Pundamilia pundamilia*; photo credit: P. Dijkstra); (g) greenish warbler and representative song spectrograms (from top to bottom: Siberia, Kyrgyzstan, and India; photo credit: E. Scordato); and (h) Italian and western European common wall lizard (*Podarcis muralis*; photo credit: R. Heathcote).

Male competition can lead to speciation in sympatry

One major research focus has been determining how male competition might initiate sympatric speciation or stabilize a polymorphic male trait within a species (Table 1; Figure 2a). Inspired by observations in cichlid fish, Seehausen and Schluter (2004) outlined a verbal model describing how male competition could generate disruptive, negative frequency-dependent selection on a male competitive trait. In a mostly monomorphic population, a male with a rare, novel trait (e.g., color) may receive less aggression from other males because he is not recognized as a relevant competitor. As a consequence, rare males could maintain above-average body condition, dedicate more time to courtship, and/or occupy higher quality territories than more abundant male morphs. Rare males may further benefit from female mating biases for other male attributes (e.g., condition). Next, the rare male fitness advantage would exert positive selection on females with preferences for the rare type. Mating between females with the rare preference and males with the rare trait would result in a genetic correlation between trait and preference. Finally, further coevolution between trait and preference may allow sufficient differentiation for the 2 morphs to become reproductively isolated by the time the fitness advantage of the novel trait disappears at higher frequencies. This process would be facilitated if hybrid males suffered a

disproportionate fitness cost as targets of male aggression from both parental types. A theoretical model by Mikami et al. (2004) sought to explain how ecologically similar species might coexist in the same habitat. They assumed that conspecific males compete for mating and ecological resources while heterospecific males only compete for ecological resources. If so, males that establish territories adjacent to heterospecifics have a potential fitness advantage as they lose fewer mating opportunities to conspecific neighbors. Similar to Seehausen and Schluter (2004), Mikami et al. (2004) showed that dissimilarity among territory neighbors can be adaptive and result in negative frequency-dependent selection. van Doorn et al. (2004) tested whether sexual selection could drive speciation in sympatry using individual-based simulations and numerical analysis. The models showed that sympatric speciation is possible only when male competition, female mate choice, and female–female competition together act disruptively in a frequency-dependent manner. With disruptive selection from female mate choice and female–female competition only, female preferences and male signals do not diverge simultaneously, which is required for reproductive isolation to evolve via sexual selection. Adding disruptive male competition can stabilize the polymorphism in male traits and corresponding mating preferences, enabling coexistence of male types both during and after speciation (van Doorn et al. 2004).

Table 1
Primary mechanisms responsible for divergence by male competition

Evolutionary process	How it works	Phenotype predictions	Geographic scenario	Role of ecology	Role of female choice	Examples	Internal or external selection pressures	Nature of selection
Negative frequency dependent selection	Rare morphs receive less competition, which results in a fitness advantage that facilitates invasion of new types and stabilizes existence of 2 morphs. Rare weapon types or behavioral strategies may confer an advantage in competition.	Each morph biases aggression toward own morph. Rare morph receives less overall aggression. Rare morphs are more competitive and have higher fitness.	Sympatry, Secondary contact	Environmental differences not required. Could function in absence of ecological differences; but may involve exploiting a new niche (e.g., fighting environment).	Divergent female mate choice not required but rare morph advantages in competition may exert disruptive selection on female mating preferences; Similar pattern could result from female preference for novelty.	Cichlid fish (1–3), stickleback fish (4)	N/A; this hypothesis does not predict a role of ecology.	Similar
Ecological selection	Differences in sensory environment change the transmission and reception of agonistic signals as well as competitive responses, driving signal divergence.	Divergent signals corresponding to sensory environment; conspicuous signals confer an advantage in male competition. Male competitive traits (i.e., level of aggression) vary as a function of ecology.	Sympatry, Allopatry, Parapatry	Environmental differences required. Could involve transmission/perception of signals or condition dependence, or variation in ecological selection pressures (e.g., habitat quality or abundance, fighting substrate, population density, operational sex ratio, predators, or parasites).	Divergent female mate choice not required. May exploit female sensory biases as well, but not necessary as females could base mate choice on a different trait.	Stickleback fish (4, 8, 9), Anolis lizards (10), greenish warblers (11)	External: changes in the transmission environment lead to signal divergence to increase signal detectability. Internal:	Divergent
Mutation-order	Different mutations (alleles) fix in each population adapting to similar selection pressures.	In reciprocal transplants, males from each population should be equally competitive in both habitats. In simulated secondary contact, a male should have equal competitive success against heterotypic or homotypic male, assuming heterotypic signals/weapons are competitively compatible (Figure 5; Mendelson et al. 2014).	Allopatry	Environmental differences not required. While ecology may still shape the evolution of signals and weapons, it does so similarly in both populations.	Divergent female mate choice not required; Selection favoring male competitive phenotype might facilitate the evolution of female preferences for that phenotype.	Darter fish (5, 6), amazonian birds (7)	Internal or external: inherently not possible to make a prediction.	Similar

Table 1 *Continued*

Evolutionary process	How it works	Phenotype predictions	Geographic scenario	Role of ecology	Role of female choice	Examples	Internal or external pressures	Nature of selection
	Other environmental differences (e.g., in habitat quality [or abundance], fighting substrate, population density, operational sex ratio, predators, or parasites) influence resource defendability and the relative cost and benefits of using certain competitive traits in agonistic interactions, favoring different competitive phenotypes.				Female preferences may act in concert with male competition (e.g., females prefer winners of contests) and enhance divergence, or oppose competition (e.g. females choose males based on non-competitive traits) and slow divergence.		Natural selection imposed by changes in the environment leads to divergence in male strategies for competing with other males or attracting mates.	
Agonistic character displacement	Selection to reduce competition between species results in shifts in competitive phenotypes (divergent or convergent). When interspecific competition for mates or breeding sites is low, negative frequency dependent selection, resulting from males biasing aggression to conspecifics, could facilitate species coexistence.	Heterotypic differences in competitive phenotypes are more pronounced in sympatry than allopatry. Each phenotype biases aggression to homotypics. Intermediate phenotypes receive more aggression than parental phenotypes	Secondary contact	Environmental differences not required. Environmental factors can limit or favor the change in agonistic characters (e.g., conspicuous coloration).	Divergent female mate choice not required. Selection from female mate choice could facilitate divergence of male traits (if females similarly select on the same traits in mate choice as males recognize), or limit divergence of male traits (if selection from females acts in opposition on male competitor traits.	Rubyspot damselflies (12–14), <i>Ficedula</i> flycatchers (15)	Internal: selection against hybridization leads to phenotypic divergence.	Reinforcing

For each of 4 major evolutionary mechanisms by which male competition might lead to speciation, we outline how the mechanism works, what outcomes it predicts for competitive phenotypes, consider geographic scenario(s) under which it is most likely, and consider the roles of interactions with ecology and mate choice. Finally, we align the mechanisms of male competition driving speciation with existing speciation by sexual selection frameworks that are organized by nature of selection (Langerhans and Riese 2013; Mendelson et al. 2014), and consider whether selection pressures driving divergence in male competitive phenotypes are internal or external (Safran et al. 2013, and similarly Maan and Seehausen 2011). Nature of selection frameworks considers 3 mechanisms of speciation by selection: similar selection (reproductive isolation resulting from different evolutionary responses to similar selection pressures), divergent selection (reproductive isolation resulting from evolutionary responses to divergent selection), and reinforcement selection (reproductive isolation stemming from selection to avoid mating between populations). Selection is internal when it acts on signals or competitive phenotypes directly, or through pleiotropy or linkage disequilibrium and external when acting on the transmission or reception of signals (Safran et al. 2013). (1) Seehausen and Schluter 2004, (2) Dijkstra et al. 2006, (3) Dijkstra et al. 2007, (4) Bolnick et al. 2016, (5) Martin and Mendelson 2012, (6) Martin and Mendelson 2016a, (7) Winger 2017, (8) Lackey and Boughtman 2013, (9) Tinghitella et al. 2015, (10) Leal and Fleishman 2004, (11) Scordato 2017, (12) Anderson and Grether 2010a, (13) Grether et al. 2013, (14) Grether et al. 2009, (15) Vallin et al. 2012.

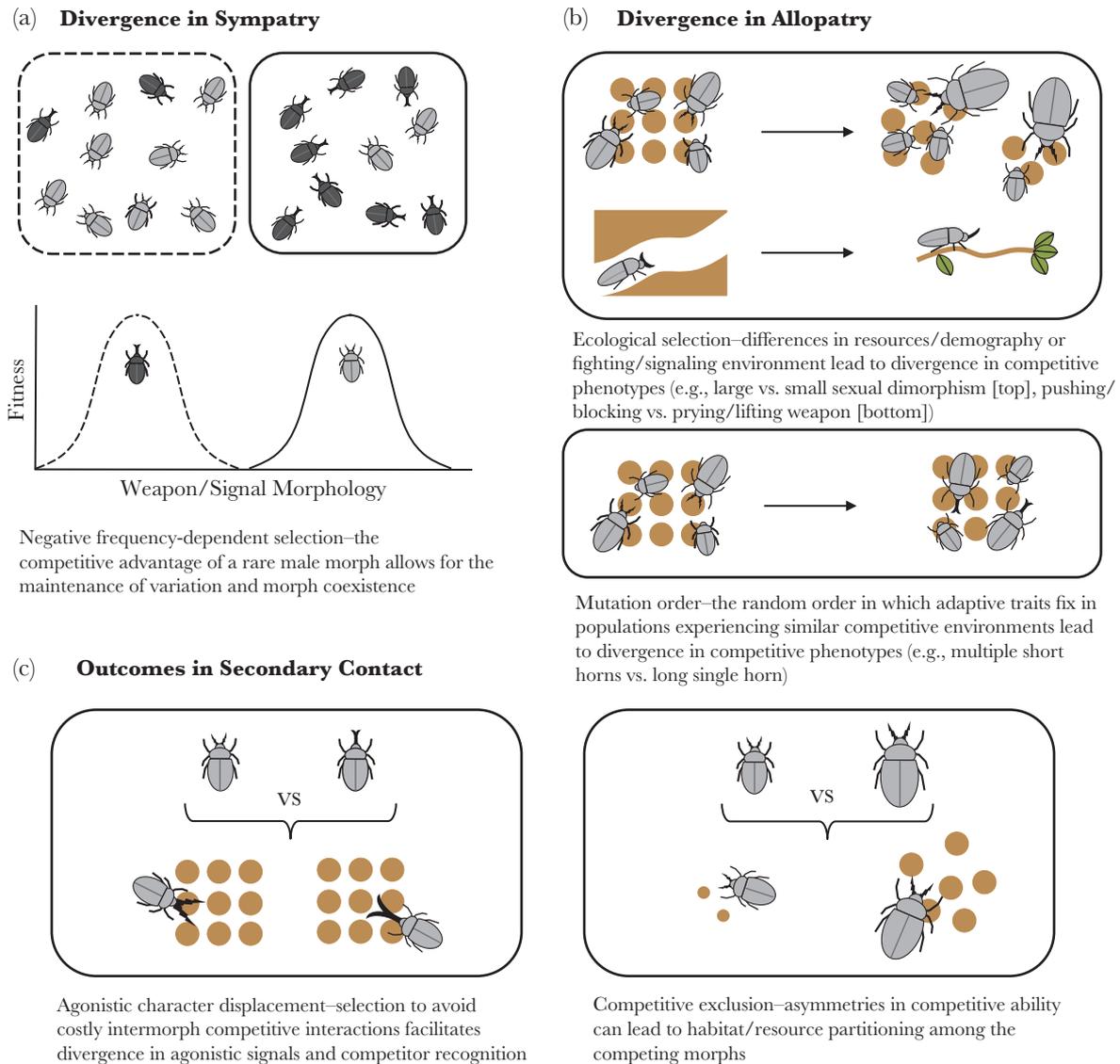


Figure 2
Mechanisms hypothesized to drive divergence in male competition in sympatry, allopatry/parapatry, and secondary contact. Until recently, work on speciation by male competition focused on sympatric geographic contexts. (a) In sympatry, negative frequency-dependent selection that favors rare morphs can allow novel competitive phenotypes to become established in a population as well as maintain 2 morphs. (b) More recent work expands the circumstances in which male competition is important for speciation to include divergence in competitive phenotypes in allopatry via differences in ecological selection (top) or mutation order between populations (bottom). (c) During secondary contact male competition may contribute to speciation through agonistic character displacement or competitive exclusion.

Empirical support for a role of male competition in sympatric speciation comes primarily from cichlid fish, a model system for studying adaptive radiation (Seehausen 2006). Seehausen and Schluter (2004) presented field data showing: 1) closely related Lake Victoria haplochromine cichlids tended to co-occur if males of those species were differently colored, and 2) territory holders within a breeding site were found more often near dissimilarly colored males. Continued work in cichlids (Figure 1b,f) suggests that males often bias their aggression towards homotypic males, though results are mixed (Dijkstra et al. 2006, 2007; Pauers et al. 2008; Tyers and Turner 2013; Magalhaes et al. 2013; Lehtonen 2014). This pattern is most pronounced early and late in divergence (Dijkstra et al. 2007), but can be asymmetric (i.e., only one male type exhibits aggression bias; Dijkstra et al. 2006). Aggression biases, along with intrinsic competitive advantages (Dijkstra et al.

2005) and female mate choice influenced by male traits and territory quality (Dijkstra et al. 2008), could aid a novel, rare male type during early invasion and as morph frequencies equilibrate.

Although a focus of current theory, disruptive selection on male competitive traits need not be associated with rare male advantages in male competition. One example comes from limnetic and benthic 3-spine stickleback fish species pairs (Figure 1c), which are a well-studied example of ecological speciation (McKinnon and Rundle 2002). In F₂ populations of limnetic and benthic 3-spine stickleback fish species (*Gasterosteus aculeatus* spp.; Figure 1c), male competition favors divergence in sympatry without negative frequency-dependent selection: rare male phenotypes did not appear to have an advantage and, in fact, were selected against by male competition (Keagy et al. 2016). Disruptive selection from male competition favored 2 phenotypic optima that correspond to the trait combinations in wild limnetic and benthic

species, and was amplified by differences in nesting habitat (Lackey and Boughman 2013) and population density (Keagy et al. 2016).

Male competition can drive divergence in allopatry

Though much work initially focused on how male competition contributes to the evolution and persistence of different morphs in sympatry, recent work has begun to consider when and how male competition contributes to divergence in allopatry and parapatry. We lack a theoretical and mechanistic framework specific to divergence via male competition in allopatry, but mechanistic frameworks explaining allopatric divergence in female choice (Safran et al. 2013; Mendelson et al. 2014) are particularly relevant. Generally, allopatric divergence in sexually selected traits stems from differences in the environment (e.g., variation in operational sex ratio, population density, climate, biotic interactions, signaling environments, and habitat complexity) or chance events (i.e., founder effects and mutation-order processes). Population demographics may be similarly important in shaping male competition strategies (Table 1, Figure 2b). Emlen and Oring (1977) predicted that patchily distributed resources, asynchronous breeding, and male-skewed operational sex ratios lead to an increase in (typically male) competition for access to matings. Empirical data often support these predictions: studies have found that the intensity of aggressive precopulatory male competition behavior within populations varies as a function of resource availability (Kolluru and Grether 2005; Wauters et al. 2005; Reichard et al. 2009), operational sex ratio (Kvarnemo and Ahnesjö 1996; Kokko and Rankin 2006; Weir et al. 2011; Wacker et al. 2013), population density (Jirotkul 1999), and breeding synchrony (Grant et al. 1995; Hammers et al. 2009). In greenish warblers (*Phylloscopus trochiloides*; Figure 1g), for instance, male songs and aggressive responses have diverged in parapatric populations surrounding the Tibetan plateau that differ in food availability and population density (Irwin 2000; Irwin et al. 2001). These environmental gradients also predict differences in the intensity of male aggression and seasonal patterns of territoriality between populations (Scordato 2017).

Agonistic signals and behavior may also diverge when environments differ in trophic interactions and resource availability (e.g., predators, parasites, and prey; Table 1). A rich body of literature describes how predators and parasites shape conspicuous sexual signals and behavior (Zuk and Kolluru 1998). Competitive phenotypes may vary across environments that differ in the local abundance of predators and parasites, with less conspicuous signals and behavior expected when risk of mortality to predators/parasites is high (Zera and Harshman 2001; Qvarnström et al. 2012). Island populations of the strawberry poison-dart frog (*Oophaga pumilio*) differ in color patterns that function in male competition (Crothers et al. 2011; Cummings and Crothers 2013; Crothers and Cummings 2015) where predators and availability of prey items responsible for frog toxicity also differ (Maan and Cummings 2012; Cummings and Crothers 2013; Dreher et al. 2015). Similarly, the presence of acoustically-orienting parasites led to the loss of male singing ability in some populations of the field cricket *Teleogryllus oceanicus* (Zuk et al. 2006), with implications for mate choice (Tinghitella et al. 2009; Tinghitella and Zuk 2009) and male competition (Logue et al. 2010). Finally, resource availability and diet also influence the cost of expressing competitive traits (Grether 2000). For instance, the costs of developing carotenoid-based coloration, which depends on absorption from food (Svensson and Wong 2011), may vary

across allopatric populations that differ in carotenoid availability, potentially leading to divergence in coloration.

Environmental context may promote divergence in weapons in addition to signals (Table 1, Figure 2b). While the mechanisms of weapon divergence are poorly understood (McCullough et al. 2016), 2 hypotheses have received some support. The first posits that selection should shape weapons to be most effective for a given style of fighting (e.g., ramming, wrestling, or tossing; Lundrigan 1996; Caro et al. 2003; McCullough et al. 2014). The second posits that the costs and benefits of agonistic signals, fighting styles, or weapons may vary across environments. Dung beetle weapons, for instance, are shaped by different trade-offs that depend on their location on the head. Weapons extending from the front of the head decrease the relative size of the antenna, while weapons extending from the back of the head decrease the relative size of the eyes (Emlen 2001). These divergent costs across weapons may interact with ecological constraints (e.g., population density) to determine which weapon types are most favorable in different habitats (Emlen et al. 2005).

Sensory drive (the evolution of signals and sensory systems to maximize detectability in the environment in which they are used; Boughman 2002; Maan and Seehausen 2011; Smith et al. 2012) is traditionally studied in the context of female preferences for conspicuousness that generate environment-dependent divergence in ornaments (Maan and Seehausen 2011). However, sensory drive can also influence divergence in male competitive phenotypes because conspicuous traits can increase performance in aggressive interactions (Table 1). For instance, *Anolis* lizard dewlaps differ in color and shape across their radiation in the Caribbean islands (Nicholson et al. 2007; Ng et al. 2013). Some of these differences increase conspicuousness in certain light environments (Leal and Fleishman 2002; Leal and Fleishman 2004), and dewlap color may influence male aggressive responses to heterotypic competitors (Macedonia and Stamps 2010; Macedonia et al. 1994, 2013, 2015). Similarly, 3-spine sticklebacks have diverged in nuptial color repeatedly across western North America (McPhail 1969; Reimchen 1989; von Hippel 1999; Figure 1d), likely due to differences in light environments (Reimchen 1989; Boughman 2001; Scott 2001). Males from locations where the water is relatively clear exhibit a red throat, while those from locations with red-shifted water have lost the red throat and frequently display melanic body coloration (McPhail 1969; Scott 2001; Figure 1d). The red throat is both an agonistic (Bakker and Sevenster 1983; Rowland et al. 1995; McKinnon 1996) and a mating signal (Boughman 2001), and the change in male color appears to affect male competition, though the pattern of aggression bias with respect to color varies in the 2 instances in which it has been studied (Tinghitella et al. 2015; Bolnick et al. 2016).

Finally, chance events play an important role in divergence in allopatry (Table 1, Figure 2b). As with other traits, male competitive phenotypes can be shaped by genetic drift via founder effects and the random order in which adaptive traits fix in populations (i.e., mutation order, Mani and Clarke 1990; Schluter 2009; Mendelson et al. 2014). At least 2 systems support a role for stochasticity in divergence of competitive phenotypes. While driven at least partly by ecological context, the evolution of song structure in greenish warblers follows different trajectories via parallel paths of divergence along the eastern and western sides of the Tibetan plateau, suggesting a role for stochastic events (Irwin 2000; Irwin et al. 2001; Figure 1g). Male darters (*Etheostomatinae*; small benthic stream fish; Figure 1e) exhibit species-specific nuptial coloration that functions both as an agonistic signal (Zhou and Fuller 2016) and a mating

signal (Williams et al. 2013) within species. In the lab, aggression between allopatric species decreased as interspecific color differences increased (Martin and Mendelson 2016a). In closely related darter species, environmental differences do not explain color differences, but a positive relationship between neutral genetic divergence and color differences suggests a role for chance mutational events in similar environments (Martin and Mendelson 2012; but see Bossu and Near 2015; Ciccotto and Mendelson 2016).

Character displacement via male competition in secondary contact

When recently diverged lineages come into secondary contact after a period of allopatry, they may still share similar agonistic signals and similar responses to those signals (Schluter 2000). Selection from interspecific competition can then drive evolutionary changes in competitive phenotypes (Table 1, Figure 2c). Field observations suggest that agonistic signals and responses can either diverge or converge in secondary contact. Grether et al. (2009) used individual-based simulation models to test whether divergence or convergence of agonistic signals depends on the degree of competition between heterotypic males for access to resources or mating opportunities (i.e., reproductive interference). They found that when heterotypic males rarely compete for access to the same resources or mates, competitive signals and responses diverge via agonistic character displacement (i.e., selection against competitive interactions between heterospecifics) (Grether et al. 2009). However, when heterotypic males frequently compete for the same resources or mates, competitive signals and responses converge because heterotypic males are relevant competitors, and interspecific aggression yields the same benefits as intraspecific aggression (Grether et al. 2009; Drury et al. 2015).

Theoretical work has also examined potential outcomes for divergence when both agonistic and reproductive character displacement (i.e., selection on female mate preferences to limit costly heterospecific mating; Pfennig and Pfennig 2009, 2010) act on the same trait (Grether et al. 2013; Okamoto and Grether 2013). In genetically explicit individual-based models that allowed male signals, female mate recognition, and male competitor recognition to evolve, either agonistic or reproductive character displacement acting alone could result in rapid and persistent divergence in the male trait (Okamoto and Grether 2013). When agonistic and reproductive character displacement acted together on the same trait, divergence dynamics were driven largely by reproductive character displacement, even when agonistic character displacement was stronger (Okamoto and Grether 2013), because males are under strong selection to be recognized by conspecific females. Importantly, divergence in competitor recognition could result directly from agonistic character displacement or indirectly from reproductive character displacement. Thus, a pattern of differentiated competitive phenotypes does not necessarily imply that male competition caused divergence.

Recent empirical work also supports a role for male competition driving divergence in aggressive signals and competitive responses during secondary contact (Grether et al. 2013). Where dark-winged rubyspot damselflies *Hetaerina titia* co-occur with clear-winged congeners (*H. americana* or *H. occisa*), both male wing coloration and competitor recognition have diverged relative to allopatric populations such that interspecific competition is relatively uncommon (Anderson and Grether 2010a,b; Figure 1a). Wing pigmentation does not impact female mate preferences (Drury and Grether 2014), so reproductive character displacement is not a viable

alternative explanation for the shifts in wing coloration and competitor recognition (Okamoto and Grether 2013).

Intra- and interspecific male competition for territories in secondary contact might also result in competitive exclusion or asymmetric introgression due to differences in competitive abilities (Figure 2c). Competitive exclusion within or between species (one competitor type outcompeting another for a shared resource; Hardin 1960) could lead to local extinction of the less successful competitor and/or force the latter to use less preferred habitat (Owen-Ashley and Butler 2004; Winkelmann et al. 2014). If competitor types differ in habitat use, natural selection could further differentiate competitive phenotypes. Selection against migrants could then lead to ecological specialization and eventual speciation (Hendry 2004; Nosil et al. 2005; Rundle and Nosil 2005). Interspecific interactions drive habitat segregation between several species of birds (Jankowski et al. 2010; Freeman et al. 2016; Freeman and Montgomery 2016). For instance, male collared flycatchers (*Ficedula albicollis*) exclude pied flycatchers (*F. hypoleuca*) from preferred habitat (Vallin, Rice, Arntsen, et al. 2012). The use of different habitats by each species has led to asynchrony in breeding time (Vallin, Rice, Bailey, et al. 2012) and differences in habitat preference via imprinting (Vallin and Qvarnström 2011), both of which should strengthen reproductive isolation. In the common wall lizard (*Podarcis muralis*), intraspecific male competition contributes to asymmetric hybridization and introgression where 2 divergent lineages co-occur in secondary contact zones (While et al. 2015; Heathcote et al. 2016). Smaller males of the Italian subspecies were excluded from conspecific matings by larger males, leading to their hybridization with females from the competitively inferior Western European lineage (MacGregor et al. 2017).

Finally, negative frequency-dependent selection resulting from males biasing aggression towards conspecifics could facilitate coexistence of species upon secondary contact (Kohda 1998). However, as discussed above, aggression towards conspecific versus heterospecific males may be adaptive responses to the degree of competition between heterospecifics for resources, mates, and/or breeding sites. Interspecific aggression is also influenced by phenotypic similarity between species, with phenotypically similar species generally experiencing higher levels of interspecific interference (Tynkynen et al. 2004; Pauers et al. 2008; Drury et al. 2015).

INTERACTIONS BETWEEN MALE COMPETITION, FEMALE MATE CHOICE, AND ECOLOGY

We have shown that male competition can lead to phenotypic divergence in sympatry, allopatry, and secondary contact. Here, we ask whether existing empirical evidence supports the possibility that male competition can drive speciation on its own, or if synergistic ecological selection or mate choice are required.

The best empirically supported mechanism for male competition driving trait divergence is negative frequency-dependent selection, but even this model requires assortative mating from female choice for the evolution of reproductive isolation (Seehausen and Schluter 2004). While speciation via divergent male competition alone may be possible, interactions between male competition and other selective mechanisms are much more likely to cause speciation quickly and under a broader range of conditions (i.e., higher gene flow or weaker divergent natural selection; van Doorn et al. 2004; Nosil et al. 2009). Multiple independent sources of selection that act in concert are likely necessary for sympatric speciation (Nosil et al.

2009), and there are few examples of female mate choice alone driving speciation without the addition of ecological differences (Safran et al. 2013; Scordato et al. 2014; Servedio and Boughman 2017, but see Gray and Cade 2000; Mendelson and Shaw 2005; Boul et al. 2007). By extension, speciation solely by male competition may be unlikely or rare.

Untangling the interactions between behavioral variation (e.g., competitive ability, mate and habitat preferences) and ecology during population differentiation and speciation is complicated, especially between older species because phenotypic divergence is likely to continue after speciation has been completed (Coyné and Orr 2004). Even if reproductive isolation among closely related species arises due to divergence in male competitive phenotypes, the history of divergence in these traits is often unknown. Species boundaries may currently be maintained by assortative mate choice, but initial trait divergence driven by male competition (with or without ecological interactions; Lackey and Boughman 2013; Winkelmann et al. 2014). The interconnectedness of mate preferences, competitive phenotypes, and ecological variation, in combination with the ability of sexually selected traits to evolve rapidly, underscores the importance of studying recently diverged populations and species to identify which processes most likely initiated speciation and how those processes interact.

Recent studies clearly demonstrate that male competition and ecology can interact to drive divergence in the absence of divergent female mate choice. In common wall lizards (Figure 1h), there is no evidence that female choice is important to the maintenance of species boundaries (Heathcote et al. 2014, 2016). Instead, assortative mating between Western European and Italian subspecies in secondary contact occurs through a combination of male choice and competition, and environmentally-dependent competition dynamics affect whether the lineages remain distinct (Heathcote et al. 2016). Similarly, in riverine stickleback (Figure 1d) and Lake Malawi cichlid (Figure 1f) populations, male competitive biases likely contribute to color differentiation between types, while female preferences do not because females of both types prefer the same trait (sticklebacks: Tinghitella et al. 2015; but see Scott 2004) or show no preference under standardized lighting (cichlids: Malinsky et al. 2015). In cichlids, such lack of preference suggests that divergent mate preferences follow rather than drive divergence of male color (Malinsky et al. 2015).

In many mating systems, both male competition and female choice act either sequentially or simultaneously to influence fitness (Wong and Candolin 2005; Hunt et al. 2009). It is relatively straightforward to consider how male competition and female choice could act in concert to drive speciation if both processes favor the same alternative male trait combinations and/or females choose mates on the basis of dominance status. One well-studied example is the *Pundamilia pundamilia*-*Pundamilia nyererei* species pair of Lake Victoria cichlids. These species are sympatric but inhabit different depth ranges with corresponding differences in light environment, which likely led to divergence in visual sensitivity and male nuptial coloration, and ultimately to speciation (Seehausen et al. 2008; Seehausen 2015; Maan et al. 2017). Divergent color patterns appear to be maintained by disruptive selection from both female choice (Seehausen and van Alphen 1998; Haesler and Seehausen 2005) and male competition (Dijkstra et al. 2007; Verzijden et al. 2008). However, male competition and female choice do not always act in concert. Instead, they may act on different traits (Lehtonen and Lindström 2009), or, rarely, in different directions on the same trait (Hunt et al. 2009). The evolutionary consequences of

interactions between male competition and female choice will depend on genetic correlations between traits under selection by each mechanism. Systems in which male competition and female choice oppose one another are rare in speciation research and certainly deserve further study (Sefc et al. 2015; Svensson et al. 2016).

Finally, males and females often have different optimal reproductive strategies, and this conflict between the sexes can lead to rapid evolutionary change and even speciation (Gavrilets 2014). For example, males may evolve traits that increase mating rates, while females evolve strategies to minimize unwanted harassment. This type of interlocus sexual conflict can drive perpetual coevolutionary changes in male and female traits, which could result in divergence between populations and allopatric speciation (Parker 2006; Rönn et al. 2007). Sexual conflict arising from adaptations to ensure success in male competition is likely to result in rapid evolutionary changes in whole suites of male and female traits (Qvarnström et al. 2012). However, the role of male competition in sexual conflict and speciation is still poorly understood and is an exciting area for future research.

FUTURE RESEARCH PRIORITIES

The burgeoning body of work on male competition makes this an ideal time to articulate future research priorities. To fully integrate male competition into our understanding of speciation by sexual selection a number of important questions need answering.

When is speciation by male competition most likely?

It is advantageous to develop broad, testable hypotheses about the conditions under which male competition might play a particularly important role in diversification. First, when males can monopolize mating resources in patchy environments, polygyny is likely to evolve and male competition is consequently predicted to generate relatively strong selection (Emlen and Oring 1977). By extension, we predict that male competition is most likely to drive divergence between populations with polygynous mating systems as a result of strong male competition *within* populations. At present, most research on male competition driving divergence appears focused on polygynous or polygynandrous systems. This may reflect limited taxonomic coverage of male competition and speciation research, or it may mean that male competition is indeed more important for divergence in these mating systems. Future work on the contribution of male competition to divergence in monogamous systems would help resolve these alternatives. Second, fitness effects of competitive phenotypes can be ecologically-dependent. Investigating divergent male competition among populations that differ in key mating resources might be particularly fruitful (Scordato 2017), and we expand on this idea below. Finally, when mating resources are limited (in patchy/sparse environments) such that females benefit from access to resources guarded by males, we predict male competition and female choice to align, potentially facilitating speciation because both selective pressures operate in the same direction on the same phenotype.

What drives divergence in male competitive phenotypes?

Testing hypotheses for how environmental differences in allopatry or parapatry shape divergence in male competitive phenotypes deserves further attention, given the current emphasis on

sympatry and secondary contact. Observational field studies and manipulative laboratory and field experiments would help clarify the extent to which ecological variation contributes to divergence in male competitive traits and which ecological factors are particularly important (Lackey and Boughman 2013; Scordato 2017). Examining interactions between male competition and ecological variables such as resource patchiness (Emlen and Oring 1977; Heathcote et al. 2016), population demography (Pryke et al. 2007; Anderson and Grether 2010a; Keagy et al. 2016; Scordato 2017), species interactions (Jankowski et al. 2010; Logue et al. 2010; Drury and Grether 2014; Lehtonen et al. 2015), and transmission properties of the environment (Sullivan-Beckers and Crocft 2010) are promising starts. It will also be helpful to study how trade-offs involving competitive traits differ between environments, as the costs of expressing different secondary sexual traits can be context-dependent (Grether 2000; Emlen 2005), and context-dependent costs could drive divergence in male competitive phenotypes (McCullough et al. 2016).

Unlike divergence in allopatry, divergence in sympatry is thought to require disruptive and frequency-dependent selection. Identifying the advantages of novelty will help confirm or refute this fundamental prediction of divergence in sympatry via male competition (Table 1). These could come in the form of competitive advantages to males with novel weapons or fighting styles (McCullough et al. 2016) or receipt of less aggression by males with unfamiliar phenotypes, though the evidence for this has been mixed (Mateos and Carranza 1997; González-Santoyo et al. 2014). Additionally, animal personality (consistent individual differences in behavior, such as aggressive vs. nonaggressive phenotypes), can evolve by frequency-dependent and disruptive selection (Bergmüller and Taborsky 2010) and may facilitate sympatric speciation via male competition (Ingleby and Johnson 2014). A similar mechanism has been proposed to explain divergence of alternative reproductive tactics within populations (Taborsky 2001).

What are the relative roles of male competition, female choice, and natural selection in the speciation process?

In the relatively limited empirical work that addresses the role of male competition in driving trait divergence and speciation, we find an overrepresentation of systems in which ecology, female choice, and male competition interact. These studies may not reveal the breadth of circumstances under which male competition *can* contribute to speciation, perhaps due to a taxonomic bias toward study systems where female choice is an important mechanism. We encourage additional research in systems in which female choice plays a limited role in male reproductive success (Heathcote et al. 2016) or in which agonistic signal differences reflect differences in aggressive responses but not female mate preferences (Drury and Grether 2014; Tinghitella et al. 2015; Martin and Mendelson 2016a; Moran et al. 2017). Such research would reveal when male competition might be a stronger or faster driver of divergence and speciation than female choice and natural selection. It may also be worthwhile to revisit classic sexual selection model systems (Panhuis et al. 2001; Maan and Seehausen 2011), including hybrid zones (Harrison and Larson 2014), to reassess the role of male competition in divergence.

Although we argue for distinguishing male competition from mate choice as a mechanism of speciation by sexual selection, we discourage its study in isolation. Male competition, mate choice, and ecological competition are often interconnected as these

sources of selection can act on the same trait. Disentangling the influence of these selective forces on speciation will likely require common garden experiments, presentation of artificial or manipulated stimuli, and restricting female or male behaviors in the laboratory or seminatural settings. Yet, it is critical to closely mimic natural habitats and/or quantify ecological variation and test divergence by male competition in the field. Additionally, to distinguish between common patterns and system- or setting-specific dynamics, it will be important to compare outcomes from different taxonomic groups, different study designs (dyadic vs. group settings), and laboratory-based versus field-based studies (Dijkstra et al. 2008). Mechanistic approaches may also shed light on the degree to which sensory inputs and neural processing affect the evolution of, and interactions between, competitive and mating responses. If male and female sensory systems have shared genetic and neural underpinnings, selection acting on one sex will influence the other. Another recent approach is to calculate behavioral isolation indices that quantify the contributions of competitive and choice behaviors to mating outcomes (Martin and Mendelson 2016a; Moran et al. 2017). A framework developed recently (Safran et al. 2013) may aid researchers interested in testing the relative contributions of natural selection, sexual selection, and their interaction to genetic differentiation. To extend this framework to include male competition, one could measure morphological and behavioral traits associated with environmental differences, female choice, and male competition (e.g., agonistic signals, weapons, measures of aggression, competition biases), and additionally measure environmental differences and genetic divergence among populations/species. Multiple matrix regression and distance-based redundancy analysis then assess how genome-wide divergence across populations is explained by pairwise geographic and phenotypic distances while controlling for their spatial autocorrelation (Safran et al. 2016). Simultaneous tests of the association between reproductive isolation and male competitive traits would also provide a more direct link between male competition and the speciation process (Martin and Mendelson 2016b). Finally, theoretical work may be particularly well-suited to evaluate the conditions under which divergent natural selection and/or mate choice facilitate or hinder speciation by male competition, providing testable predictions for future empirical work. Hypothetically, male competition could drive speciation in a heterogeneous environment without female mate choice. One compelling idea is that environmental differences could favor distinct, locally adaptive competitive traits. If only the most competitive males gain access to females, even without expression of female mate preferences, divergence in the competitive trait and habitat preferences could occur where environments differ. In this scenario, speciation would become even more likely if females also prefer locally adapted male competitive traits, enhancing reproductive isolation between habitat specialists (van Doorn et al. 2009).

How do differences in competitive phenotypes lead to reproductive isolation?

Recent work on speciation by male competition has focused largely on the first steps in the speciation process (i.e., divergence in competitive phenotypes), but how male competition facilitates the evolution of reproductive isolation itself remains poorly understood. Prezygotic isolation could arise from male competition in at least 2 ways. First, increased mating effort via costly competitive interactions within species might favor the evolution of male mate choice (Edward and Chapman 2011). If male mate preferences differ between populations, prezygotic isolation may then evolve as an

indirect result of male competition. Work in 2 systems characterized by divergence in male competitive traits, darters (Martin and Mendelson 2016a) and wall lizards (Heathcote et al. 2016), suggest that male mate choice for conspecific females reduces hybridization. Identifying whether male competition commonly facilitates the evolution of male mate choice requires additional study. Second, work in sperm and pollen competition is particularly promising for understanding how postcopulatory competition for mates can cause reproductive isolation because intraspecific mating traits (e.g., seminal fluid proteins, pollen-pistil interactions) can evolve rapidly and yield reproductive isolation as a by-product (Manier et al. 2013; Castillo and Moyle 2014).

Premating male competition could also contribute to postzygotic barriers. For instance, adaptation to different competitive environments could lead to divergence in a suite of correlated traits and their underlying loci. This, in turn, could lead to Dobzhansky-Muller incompatibilities, alleles that, when combined in a hybrid genetic background, cause hybrid sterility and inviability (Dobzhansky 1937; Muller 1942; Orr and Turelli 2001). Consistent with this idea, the extent of total reproductive isolation (cumulative isolation from both pre- and postzygotic barriers) in darters correlates with the extent of differences in male color, an agonistic signal (Martin and Mendelson 2016b). Although male colors are likely the target of both male competition and female choice in darters, these findings suggest that male competition could play a part in the evolution of intrinsic barriers to gene flow like gametic incompatibility and hybrid inviability.

How does correlated evolution of male competitive traits shape speciation?

Many studies tend to focus on a single competitive trait, but it is important to note that success in male competition is influenced by multiple traits (i.e., signal/weapon characteristics, competitor recognition, and aggressive behavior) that may evolve in concert and shape the process of population differentiation and speciation. Male competitive traits can be functionally linked to other life-history traits such as immunity or antioxidant defenses (Zera and Harshman 2001), genetically linked to other seemingly unrelated traits through pleiotropy or linkage disequilibrium, or correlated with other behavioral traits (Lundigran 1996; Caro et al. 2003). For example, coordinated changes in male coloration and stress sensitivity in the melanocortin system (Ducrest et al. 2008) could facilitate speciation if alternative trait combinations are adaptive (Dijkstra et al. 2017). In addition to shared physiological mechanisms, correlated trait evolution is also driven by underlying genetic architecture. A single chromosomal inversion is likely responsible for the evolution of 3 male morphs that differ in numerous traits (testis size, steroid metabolism, behavior, body size, and coloration) in the ruff (*Philomachus pugnax*; Küpper et al. 2016; Lamichhaney et al. 2016). Additional studies of speciation with gene flow suggest that genomic regions contributing to reproductive isolation accumulate in inversions and other regions of low recombination (Burri et al. 2015; Cruickshank and Hahn 2014; Harrison and Larson 2016). If competitive traits are influenced by genes within these regions, this could facilitate the evolution of reproductive isolation. These examples beg the question of whether shared physiological or genetic mechanisms are required for divergence in competitive phenotypes, and if they accelerate or impede divergence. Advances in genomic analysis of nonmodel organisms are continuing to unravel the architecture of complex phenotypes, and will surely shed light on these topics.

How do asymmetries in competitive ability and aggression biases influence speciation?

Male competitive ability among divergent populations may be asymmetric, with one type being consistently dominant and consequently able to exclude heterotypics from high-quality habitats or displace them altogether (Owen-Ashley and Butler 2004; Pryke 2009). A recent meta-analysis found that the majority of aggressive interactions among closely related bird species are strongly asymmetric (Martin et al. 2017). Competitive asymmetry in mating contests may commonly lead to habitat isolation via competitive exclusion, but too few empirical studies exist for generalization. Alternatively, frequency-dependent social dominance (Bergmüller and Taborsky 2010) could facilitate the persistence of distinct types, but the outcomes for gene flow and/or divergence are unclear. Asymmetry in competitive abilities could also influence hybridization and asymmetric introgression, especially if female choice is weak or unidirectional (While et al. 2015; Heathcote et al. 2016). Although we understand that competitive interactions are commonly asymmetric, whether they enhance or hinder reproductive isolation between divergent forms remains to be addressed.

Divergent populations may also exhibit asymmetry in homotypic aggression biases (Dijkstra et al. 2006; Lackey and Boughman 2013). The degree of homotypic aggression can be a response to the potential threat a particular phenotype poses (Horton et al. 2012) and could arise as a consequence of asymmetries in competitive ability. Similar asymmetries in female mate choice have been interpreted as either an indication of the age of a species pair (Arnold et al. 1996) or which of 2 interacting species is ancestral vs. derived (Kaneshiro 1976, 1980). Regardless of their evolutionary origins, the consequences of these asymmetries for hybridization and speciation with gene flow are poorly understood. When homotypic aggression biases are asymmetric, other factors must stabilize the polymorphism in male competitive trait(s) during speciation, or the phenotype receiving more aggression may be driven to extinction. Whether mate choice has a role to play in mitigating these asymmetries remains to be tested.

SUMMARY AND CONCLUSION

Although research on speciation by sexual selection has been gaining traction for more than 30 years, further research focusing on the role of male competition is necessary to comprehensively explain how sexual selection contributes to phenotypic diversity, population divergence, and reproductive isolation. To motivate future work, we have described multiple mechanisms by which male competition may contribute to speciation, their predicted outcomes, and their connections with existing speciation frameworks (Table 1). Promising but understudied areas of research include studying the role of male competition in divergence in allopatry/parapatry, and working with study systems in which male competition plays a more important role in dictating reproductive success than does female choice. By evaluating when male competition *can* and *is most likely* to contribute to divergence and speciation, we will broaden and strengthen our current speciation framework.

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