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Interspecific competition, hybridization, and reproductive isolation in secondary contact: missing perspectives on males and females

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Abstract

Research on sexual selection and hybridization has focused on female mate choice and male–male competition. While the evolutionary outcomes of interspecific female preference have been well explored, we are now gaining a better understanding of the processes by which male–male competition between species in secondary contact promotes reproductive isolation versus hybridization. What is relatively unexplored is the interaction between female choice and male competition, as they can oppose one another or align with similar outcomes for reproductive isolation. The role of female–female competition in hybridization is also not well understood, but could operate similarly to male–male competition in polyandrous and other systems where costs to heterospecific mating are low for females. Reproductive competition between either sex of sympatric species can cause the divergence and/or convergence of sexual signals and recognition, which in turn influences the likelihood for interspecific mating. Future work on species interactions in secondary contact should test the relative influences of both mate choice and competition for mates on hybridization outcomes, and should not ignore the possibilities that females can compete over mating resources, and males can exercise mate choice.

Key words: female–female competition, hybridization, male–male competition, reproductive isolation, sexual selection.

Introduction

Traditional perspectives on sexual selection and hybridization

Sexual signals and mating behaviors influence whether sympatric species interbreed, and can therefore promote or impede behavioral reproductive isolation (Irwin and Price 1999; see Box 1: Definitions). Interspecific hybridization is common and is estimated to occur in 10% of animals (Mallet 2005). Traditionally, research on the role of sexual selection in hybridization has focused on the importance of mate choice and species discrimination from the perspective of choosy females, and competition from the lens of aggressive and indiscriminate males (Moore 1987; Grant and Grant 1997; Sætre et al. 1997; Parker and Partridge 1998; Wirtz 1999; Randler 2002). This conventional view considers females the gatekeepers of

species because of their greater investment in gametes and fewer opportunities for multiple mating relative to males (Bateman 1948; Andersson 1994). In contrast, males are expected to maximize fitness by mating as frequently as possible (Darwin 1871; Bateman 1948; Andersson 1994). The traditional perspective of sexual selection underlays the predictions for evolutionary outcomes in different scenarios of *secondary contact*. For instance when hybridization is maladaptive, lineages in secondary contact are expected to evolve divergence in sexually selected traits and in species recognition of mates to avoid heterospecific mating, a process known as reinforcement (Coyne and Orr 1989; Servedio and Noor 2003). The predictions for reinforcement have been developed from the perspective of females, who face higher fitness costs of heterospecific mating mistakes and are therefore predicted to discriminate more strongly

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Box 1. Definitions

Agonistic character displacement: divergence in competitive signals or traits in sympatry to reduce costly interspecific interactions.

Asymmetric introgression: the unidirectional exchange of alleles from 1 species to another.

Behavioral reproductive isolation: reduced gene flow due to divergent mating signals and preferences.

Competitive asymmetry: the superior competitive ability and/or dominance of 1 species over another.

Heterosis: hybrid vigor, when hybrids are competitively superior to their parental species.

Introgressive hybridization: interbreeding between 2 distinct lineages that results in gene flow.

Hybrid swarm: hybridization that erodes parental species boundaries.

Interspecific intrasexual conflict: antagonistic coevolution between males and females of interacting species.

Reproductive character displacement: divergence in mating signals or traits in sympatry to reduce costly interspecific mating.

Interspecific reproductive competition: competition for mates and/or mating resources between species.

Reproductive exclusion: sexual interactions between species that cause one to become locally extinct.

Secondary contact: Geographic overlap between 2 genetically distinct lineages that derived from a common ancestor and underwent a phase of allopatric isolation.

Social selection: a form of selection resulting from all social interactions in order to gain access to resources, including but not limited to mates.

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against heterospecifics than males (Sætre et al. 1997; Parker and Partridge 1998; Wirtz 1999; Servedio et al. 2009; Hudson and Price 2014). An open question is to what extent does male–male competition between lineages influence hybridization outcomes in secondary contact, and when is female mate choice predicted to support or oppose these outcomes?

Recent empirical and theoretical work has brought increasing attention to the function of male–male competition in speciation (Doorn et al. 2004; Seehausen and Schluter 2004; Dijkstra et al. 2007; Qvarnström et al. 2012; Drury et al. 2016). Reproductive competition, also known as intrasexual selection, is a component of sexual selection that involves fighting over mating resources such as territories and mates. Competition is an important determinant of mating success for many taxa, especially those with polygynous or polyandrous mating systems where reproductive success is highly skewed toward dominant individuals (Emlen and Oring 1977; Clutton-Brock 2007). Interspecific competition is common (Peiman and Robinson 2010), and *interspecific reproductive competition* can occur when species compete for shared territorial and/or signaling space involved in mate attraction and reproduction (Grether et al. 2009; Burdfield-Steel and Shuker 2011; Pfennig and Pfennig 2012). Low fitness costs to heterospecific mating for males can facilitate *introgressive hybridization* when males compete over heterospecific mates via male–male competition (Arnqvist and Rowe 2005), but

this can result in high reproductive costs for females, termed the so-called "satyr effect" (Ribeiro and Spielman 1986). Interspecific male–male competition is not widely considered to promote reproductive isolation except as it relates to female choice (but see 1B, *Competitive asymmetry and reproductive exclusion*).

Rapid divergence in sexually selected traits between closely related lineages in allopatry can promote reproductive isolation through the maintenance of species-specific signals and recognition when these lineages come into secondary contact (Coyne and Orr 2004; Hudson and Price 2014; Weber and Strauss 2016; Cooney et al. 2017). Character shifts in sexual traits can also result from species interactions in secondary contact. These processes have been widely explored in terms of interspecific male–female interactions concerning reinforcement of male traits and female recognition of those traits (see 1A, *Character displacement: ecological, reproductive, and agonistic*). However, interspecific male–male interactions can also impact the evolution of sexual traits, which in turn can influence hybridization outcomes. For instance, when lineages that compete over similar ecological and/or mating resources come into contact, their competitive interactions can cause selection on traits that influence fighting ability and competitor recognition, which can subsequently influence the evolution of reproductive isolation and/or facilitate hybridization. This process, known as *agonistic character displacement* (ACD), can result in either divergence or convergence of phenotypic traits involved in competitor recognition and fighting ability, depending on the intensity of resource competition between species (Grether et al. 2009). Divergence in competitor signals and recognition is expected to promote reproductive isolation (see Figure 1, conceptual framework). However, even species with diverged competitive traits may hybridize if males of the dominant species (e.g., the lineage that is superior in aggression, body size, and/or competitive ability) monopolize mating resources shared with males of the subordinate species. Convergence in competitive signals is expected to facilitate territorial interactions over shared, limited resources, but can also increase the likelihood of hybridization if those signals also play a role in mate recognition. Alternatively, convergence that results in the exclusion of 1 species could promote reproductive isolation. In addition to male trait evolution, female mate preferences may diverge or utilize a different sexual trait to avoid hybridization (Hankison and Morris 2003; Seddon and Tobias 2010; Hudson and Price 2014).

Updating perspectives on sexual selection and hybridization

Studies on mating behavior and hybridization often draw a dichotomy between competitive males mating indiscriminately and choosy females limiting heterospecific mating. This dichotomy is oversimplified in several ways. For instance, male mate choice can facilitate mate discrimination within and between *Timema* stick insects (Arbuthnott and Crespi 2009), thereby reducing interspecific gene flow. Additionally, females can prefer heterospecifics when they resemble high-quality conspecifics and/or ancestral preferences have not diverged, as in female orange-backed fairy wrens *Malurus melanocephalus melanocephalus* that prefer red-backed males resembling another subspecies *M. m. cruentatus* (Baldassarre and Webster 2013) and in female tungara frogs (*Physalaemus pustulosus* species group) that prefer call features of heterospecific males (Ryan and Rand 1993). In this review, I propose that we have overlooked an additional component of sexual selection that could influence hybridization and reproductive isolation in secondary contact: female–female competition.
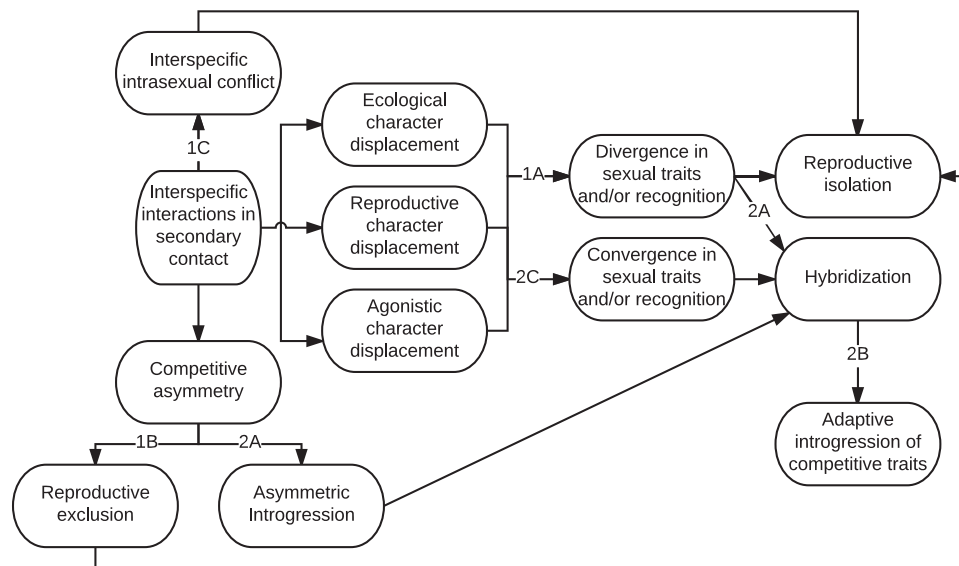
Figure 1. Conceptual framework of how competition between species in secondary contact can promote reproductive isolation and/or hybridization. Path labels (e.g., 1A) correspond to sections throughout the manuscript.

Despite a growing understanding of male–male competition and speciation, empirical and theoretical studies on the roles of female–female competition as well as male mate choice in hybridization are lacking (but see Wong et al. 2005; Servedio 2007; Kozak et al. 2009; Roberts and Mendelson 2017). There are many studies demonstrating that females compete over mating resources (reviewed in Rosvall 2011; Cain and Ketterson 2012) and males can be choosy of mates (reviewed in Kraaijeveld et al. 2007; Edward and Chapman 2011). Empirical studies across a wide variety of taxa including fish, lizards, and birds suggest that female aggression is adaptive in a number of social contexts (Stockley and Campbell 2013) including territory defense (Woodley and Moore 1999; Desjardins et al. 2006; Gill et al. 2007; Reedy et al. 2017) and reproductive success (While et al. 2009). Likewise, adaptive mate choice has been demonstrated for males in several insect species that face high reproductive costs such as sperm limitation and choose among females that vary in quality of signals advertising fecundity (Bondouriansky 2001; Nandy et al. 2012). As little attention as female competition and aggression have received in the literature, the role of female–female competition in hybridization has received far less. As a first step to addressing this gap, we need to compare the evolution of competitive traits and recognition in females to those of males, and predict the potential outcomes for hybridization in secondary contact. Future work should also focus on the role of male mate choice in speciation, but the current review will focus on comparing interspecific male–male and female–female competition.

Here, I examine the role that interspecific reproductive competition plays in hybridization, specifically between closely related lineages (species, subspecies, and divergent populations) in secondary contact when reproductive isolation is incomplete. Other reviews have focused on the diversifying role of male–male competition in promoting speciation (e.g., Qvarnström et al. 2012), but here I expand this perspective to improve our understanding of both male–male and female–female competition and their evolutionary outcomes in secondary contact, which can either facilitate or impede reproductive isolation (see Figure 1, conceptual framework). I review the empirical and theoretical evidence supporting evolutionary scenarios in which 1) competition promotes reproductive

isolation and 2) competition facilitates introgression—the exchange of alleles from one species to another. I also emphasize that the outcomes of interspecific interactions in secondary contact should be considered in the context of both competition and mate choice, as well as from the perspectives of both the signaler and the receiver, and I review what may be the first case of female–female competition promoting hybridization (Figure 2).

When Competition in Secondary Contact Promotes Reproductive Isolation

Sexual selection can be a diversifying force in driving the evolution of traits involved in mate choice and competition for mates both within and between species (Lande 1981; Panhuis et al. 2001; Coyne and Orr 2004; Ritchie 2007). Closely related lineages are often more divergent in secondary sexual characteristics than other phenotypic traits (West-Eberhard 1983; Allender et al. 2003). Sexual characteristics specifically involved in competition include those directly used in fighting, such as body size and weaponry, as well as traits important in signaling dominance, such as coloration and vocalizations (Andersson 1994). Along with divergence in agonistic signals, the visual and auditory sensory systems that receive and recognize these signals may also diverge between heterospecific competitors (Peiman and Robinson 2010; Pfennig and Pfennig 2012; Okamoto and Grether 2013). Because these sexual traits are often used both to attract mates as well as to compete for mating resources (Berglund et al. 1996), their divergence between species can have consequences for reproductive isolation. For instance, character divergence that reduces interspecific interactions will limit gene flow between species. Below I describe patterns of divergence in competitive traits and recognition resulting from interspecific interactions, and explore how this divergence can promote reproductive isolation via reproductive exclusion and sexual conflict.

Character displacement: ecological, reproductive, and agonistic

Character shifts in competitive traits and competitor recognition could take place due to different sexual, social, and ecological
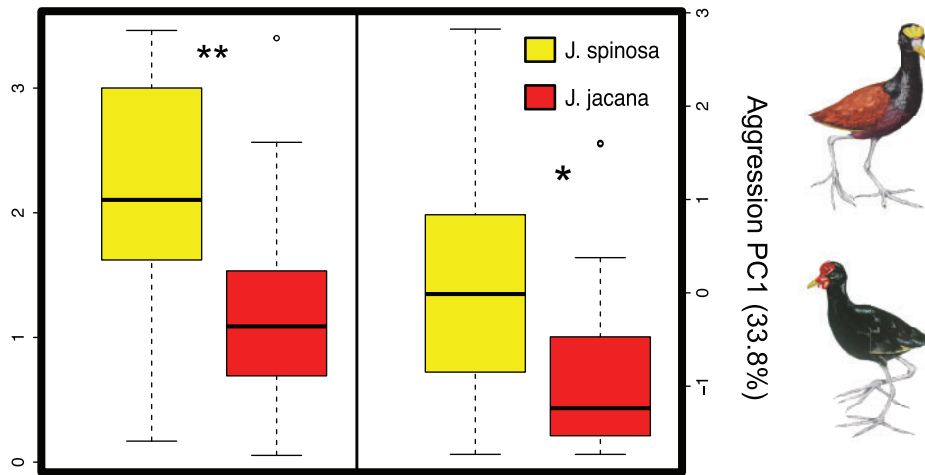
Figure 2. Females of 2 polyandrous, sex-role reversed shorebird species that hybridize in Panama show competitive asymmetries in morphology (left panel) and aggressive behavior (middle panel). *J. spinosa* females (right panel top) have larger body mass, longer wing spurs used for fighting, and are more aggressive than *J. jacana* females (right panel bottom), which may explain the asymmetric introgression of mtDNA in the hybrid zone. Figure adapted from Lipshutz (2017). Illustrations by Stephanie McClelland.

selection pressures on each lineage evolving independently in allopatric isolation (Rice and Pfennig 2007), or to selection pressures occurring from contact with a heterospecific in sympatry (Grether et al. 2009; Pfennig and Pfennig 2009). Three main processes of trait shifts due to interspecific interactions are ecological character displacement (ECD), reproductive character displacement (RCD), and ACD, and they can result in either divergence or convergence in sympatry (Grant 1972). Competitive ecological interactions in secondary contact have been widely explored (reviewed in Pfennig and Pfennig 2012; Weber and Strauss 2016). ECD is a process that produces greater shifts in ecological niches of species in sympatry than in allopatry. ECD can arise when disruptive selection causes coexisting species to diverge in their ecological niches, thereby reducing interspecific competition over a previously shared ecological resource such as food (Brown and Wilson 1956; Losos et al. 2000; Schluter 2001). Both the resource utilized and trait associated with the resource use are expected to change between the sympatric species (e.g., prey type and jaw morphology in larval feeding of spadefoot toads *Spea bombifrons* and *Spea multiplicata*; Pfennig and Murphy 2003). Divergent ECD is predicted to promote reproductive isolation in several ways. The divergence in resource acquisition traits may reduce contact between species, and therefore impede interspecific gene flow (reviewed in Coyne and Orr 2004; Price 2008). Additionally, ecological divergence between sympatric species can drive divergence in sexual signals, which can lead to reproductive isolation. In Darwin's finches, for example, ecologically adaptive divergence in beak morphology is correlated with divergence in song, which is used in territorial defense and mate choice (Huber and Podos 2006; Podos 2010). In the medium ground finch *Geospiza fortis*, large and small beak morphs demonstrate positive assortative pairing, and gene flow is reduced between morphs (Huber et al. 2007). If offspring produced by matings between these populations are intermediate in phenotype and therefore are competitively inferior in either niche, ecologically dependent postmating isolation can evolve (Pfennig and Rice 2007; Rice

and Pfennig 2010) which could initiate the speciation process (Schluter 2001; Pfennig and Pfennig 2009).

For closely related species in secondary contact that have not diverged in their secondary sexual characteristics, similar mating signals can result in species recognition errors and heterospecific mating (Gröning and Hochkirch 2008), which can in turn lead to the evolution of RCD. RCD is a process that selects for greater sexual trait divergence and/or species discrimination in sympatry compared with allopatry, and can be indicative of the reinforcement process. Much empirical and theoretical research has investigated how selection resulting from mate misrecognition and maladaptive hybridization can drive divergence in mating signals and/or preferences (Ptacek 2000; Coyne and Orr 2004; Pfennig and Pfennig 2009). Like ECD, RCD can minimize interspecific contact, including reproductive competition, if the traits that diverge also function in competitive interactions. Both ECD and RCD can influence each other, when species that compete for ecological resources also have similar sexual signals (reviewed in Pfennig and Pfennig 2009). Species discrimination between divergent signals can be tested using playback experiments, but their implementation and interpretations can be challenging for both male and female behavior (see Box 2).

Similarity in agonistic signals and competitor recognition can also select for divergence or convergence between species in secondary contact, a process known as ACD. ACD evolves to reduce maladaptive interspecific competition over mating resources (Grether et al. 2009), and can change the degree and/or outcome of interspecific interactions (Cody 1969; Grether et al. 2013). ACD has received relatively less attention than ECD and RCD, and fewer empirical cases are known. In the rubyspot damselfly genus *Hetaerina*, males of some species use wing coloration for competitor recognition, and similarity in male wing coloration causes misidentification between species (Anderson and Grether 2010a). Observational and experimental studies revealed that interspecific territorial aggression in sympatry selected for shifts in agonistic signals (Anderson and Grether 2010a) and competitor recognition (Anderson and Grether 2010b). Similar patterns have been found in

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Box 2. Interpretation of playback experiments

To experimentally measure the extent of premating reproductive isolation between 2 species, studies compare mating signal divergence along with relative responses, that is, discrimination, between conspecific and heterospecific signals. For paired design playback studies in which males discriminate between conspecific and heterospecific stimuli, this is interpreted as evidence for reproductive isolation because divergent mating signals would reduce heterospecific gene flow (Baker 2001; Slabbekoorn and Smith 2002; Podos 2010; Lipshutz et al. 2017). Males whose territorial signals are not recognized by neighboring heterospecifics will face difficulty establishing and defending their territories in sympatry (Searcy and Nowicki 2005), which could promote reproductive isolation if they are forced to set up territories elsewhere. Tests in sympatry often reveal that males do not discriminate between heterospecific and conspecific signals—this is interpreted as lack of a behavioral barrier, which could promote hybridization (Gee 2005; den Hartog et al. 2008).

Male white-crowned sparrow responding to simulated territorial intrusion during playback experiment. Photo by Elizabeth P. Derryberry.

For the majority of playback studies it is common to test only 1 sex, males, and indirectly infer similar signal discrimination and/or preference by females. This practice is prevalent because it is easier to conduct male playback experiments than female preference experiments in many taxa. However, such an interpretation of discriminatory response is problematic, in that it assumes that the relative salience of conspecific and heterospecific signals to an individual territory holder is a suitable proxy for female discrimination and even female preference. While male signals can be important for both male–male competition and female choice, the 2 sexes may not have evolved the same discriminatory abilities, nor should we expect them to respond similarly to a potential heterospecific competitor versus a potential heterospecific mate. We should therefore be interested in the direct value of territorial playback experiments—for understanding species recognition in territorial defense, rather than indirectly interpreting tendency for reproductive isolation between males and females. To understand how male and female discrimination between conspecific and heterospecific sexual signals compare, we should explicitly test responses in both males and females of the same species. One successful example of this is a recent study in the *Ficedula* flycatchers, which found that females discriminate between conspecific and heterospecific sexual signals in sympatry, whereas males did not (Wheatcroft and Qvarnström 2017). Given that sexual signals are often multimodal (e.g., acoustic and visual) and multicomponent (e.g., multiple messages encoded) (Hebets and Papaj 2005), future work should also test the relative salience of specific components of signals for species recognition in males versus females.
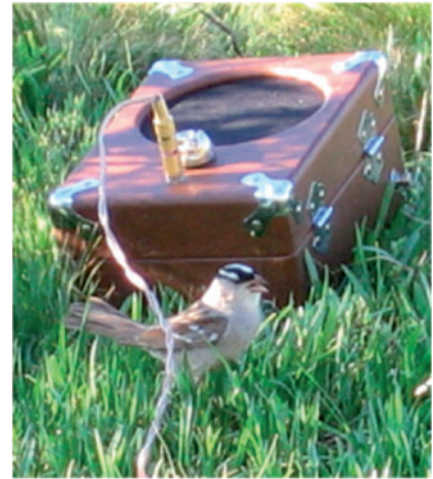
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the auditory signal reception of dendrobatid frogs *Allobates femoralis* (Amézquita et al. 2006) and the male nuptial color of three-spined sticklebacks (*Gasterosteus aculeatus* spp.) (Albert et al. 2007). One open question is whether the character shift is expected to occur more often for the competitively inferior species, due to selection for access to resources monopolized by the dominant species.

Divergence in competitive signals also involved in mate recognition can promote reproductive isolation if females discriminate between these species-specific competitive signals and prefer to mate with conspecifics (Okamoto and Grether 2013). In the hybrid zone between pied flycatchers *Ficedula hypoleuca* and collared flycatchers *Ficedula albicollis*, both ACD and RCD may explain a divergence in male plumage in sympatry, which both reduces heterospecific aggression and heterospecific pairing. Brown morph *F. hypoleuca* males are found in sympatry with competitively dominant and black *F. albicollis*, and they receive less interspecific aggression than *F. hypoleuca* black morphs (Sætre et al. 1993; Alatalo et al. 1994). Female *F. hypoleuca* prefer brown conspecifics in sympatry with *F. albicollis*, but prefer black conspecifics in allopatry (Sætre et al. 1997; Sæther et al. 2007). Because the same traits are often used for species recognition by both potential competitors and mates (Berglund et al. 1996), disentangling ACD from RCD and

ECD can be difficult and these processes may not be mutually exclusive (Grether et al. 2009; Okamoto and Grether 2013). For instance, character displacement in bill morphology, male song, and response to song have been demonstrated between sympatric species of African tinkerbirds *Pogoniulus bilineatus* and *P. subsulphureus* (Kirschel et al. 2009), but the mechanism driving character displacement is not known. Clear cases of ACD must demonstrate that divergence in male traits is due to competition over mating resources, and not due to selection for species-specific mate recognition by females (Okamoto and Grether 2013), which has been shown in the *Hetaerina* damselflies (Drury and Grether 2014). The traditional perspectives of sexual selection emphasize RCD on male sexual traits and female recognition, and ACD on male agonistic traits and recognition (see Figure 1, pathway 1A of conceptual framework). An apparent knowledge gap is whether RCD can occur on female sexual traits and male recognition, and ACD can occur for female agonistic traits and competitor recognition. Evidence is likely to be found in systems where male exercise mate choice and females compete over shared mating resources.

Competitive asymmetry and reproductive exclusion

Divergence in competitive morphology and behavior of lineages in allopatry can result in the superior competitive ability of one lineage

over the other upon secondary contact. A recent review found that most aggressive interactions between closely related bird species were asymmetric (Martin et al. 2017). *Competitive asymmetry* that reduces interactions between species can lead to reproductive isolation. For instance, if one of the species is a superior competitor and resources are limited, the dominant species may displace the subordinate species via competitive exclusion (Gause 1934; Hardin 1960). The expectations for ecological competitive exclusion are similar to those for *reproductive exclusion*, also known as sexual exclusion—when the dominance of one species in monopolizing territories and mates displaces the less competitive species and excludes them from establishing residence in sympatry (Kuno 1992; Hochkirch et al. 2007; Gröning and Hochkirch 2008). As the outcome of both ecological competitive exclusion and reproductive exclusion is that the species cannot coexist (Pfennig and Pfennig 2012), local extinction that reduces interspecific interactions could promote reproductive isolation between populations. For example, an experiment with *Callosobruchus maculatus* and *C. chinensis* weevils demonstrated that indiscriminate male mating attempts toward heterospecifics, linked with intolerance by female *C. maculatus* females, resulted in reduced reproduction, population decline, and local extinction of *C. maculatus* (Kishi et al. 2009). The expansion of a more dominant and/or invasive species' range, exacerbated by anthropogenic changes such as habitat modification and climate change, can accelerate the geographical displacement of a less dominant species (Rhymer and Simberloff 1996; Krosby et al. 2015). When the species co-occur throughout their distribution, or the more dominant species expands its range (Canestrelli et al. 2016), the less dominant species could become locally extinct (Duckworth 2008; Pfennig and Pfennig 2012). In a simulation study, the competitive ability of a native plant species via faster pollen-tube growth rates and enhanced seedling competition was predicted to prevent the risk of extinction due to both natural hybridization with invading plant species and competition with hybrids and invasives (Wolf et al. 2001). Species that are already rare are more vulnerable to extinction by hybridization (Levin et al. 1996). Reproductive exclusion is expected to promote reproductive isolation, but examples are limited. Evidence of this process is likely difficult to observe in nature because it does not leave a genetic trace, as is the case with hybridization.

The consequences of male–male competition for reproductive exclusion and reproductive isolation are likely to be similar in female–female competition, if females of one species outcompete another for mating resources, for example territories for breeding. Female–female agonistic interactions that occur within species have been predicted to promote diversification and incipient speciation. Females of some haplochromine cichlid species with bright coloration are territorial and aggressive, and use color as a cue in social interactions (Seehausen et al. 1999). An experimental assay in the cichlid species *Neochromis omnicaeruleus* demonstrated that females bias aggression toward females of their own color morph (Dijkstra et al. 2009). *Neochromis omnicaeruleus* exhibits mutual mate choice (Seehausen et al. 1999), and females compete for males of the same morph. Furthermore, female coloration is associated with behavioral dominance among female morphs (Dijkstra et al. 2009). How competitive interactions between females of the same species compare to female competition between 2 species, and whether both of these processes are expected to contribute to diversification and reproductive isolation, is an exciting avenue for future research.

Interspecific intrasexual conflict

Agonistic interactions can occur not only between the same sex of different species (e.g., male–male and female–female interspecific interactions), but also between males and females of different species (e.g., female–male interspecific interactions). Female aggression against male heterospecifics can promote reproductive isolation. For example, females at risk of interspecific pairings between salmon and brown trout showed higher rates of aggression against heterospecific males and reduced the number of eggs available for spawning (Beall et al. 1997). In other cases, however, females are unable to exert conspecific mate choice, for example in insect and waterfowl species where males force copulations (Mckinney et al. 1983; Arnqvist and Rowe 2002). This antagonistic coevolution between females and males is known as sexual conflict, when the 2 sexes have different evolutionary interests (Parker and Partridge 1998). Within species, sexual conflict can be a driver of speciation, and can promote rapid evolutionary divergence of reproductive traits (Arnqvist et al. 2000; Martin and Hosken 2003). For instance, sexual conflict can result in antagonistic coevolution of genital morphology as well as color signaling and perception, resulting in sexual polymorphisms (Hosken and Stockley 2004; Brennan et al. 2010; Gavrilets 2014). Female *Ischnura ramburii* have evolved male visual mimicry to resist male harassment, which can promote mate recognition errors by males (Gering 2017). A color polymorphism in the wing patterns of *Colias* butterflies allows females with the rare "alba" morph to avoid reproductive interference, as a means of resistance to interspecific male mating harassment (Nielsen and Watt 2000). Female sexual polymorphisms due to variation in resistance or toleration of unwanted mating could lead to speciation, but this has largely been explored within a species (Svensson et al. 2009). *Interspecific sexual conflict*, between males and females of different species, could occur if heterospecific mating promoted by indiscriminate males is opposed by female preference for conspecifics. There are several cases of forced copulations resulting in hybrids (Randler 2005; Rohwer et al. 2014) but it is unknown whether females have evolved postmating divergence in genital morphology or other traits to avoid coercive heterospecific mating. To what extent does interspecific sexual conflict, involving the opposition of competition and mate choice, promote reproductive isolation between species?

When Competition in Secondary Contact Facilitates Introgressive Hybridization

Reproductive competition between sympatric lineages can also promote hybridization, if interspecific interactions over shared mating resources occur and reproductive isolation is incomplete. The previous section explained how divergence in competitive traits between lineages could lead to reproductive exclusion, but competitive asymmetry can also facilitate a dominant lineage's monopolization of breeding with both conspecific and heterospecific mates. Some patterns indicating these processes include asymmetric introgression of genetic loci and phenotypic traits, as well as moving hybrid zones. Hybridization itself can result in the superior competitive ability of hybrids relative to their parental taxa, which can further promote backcrossing. While one outcome of interspecific reproductive competition is divergence in sexual traits, competitive signals that facilitate territorial interactions can also converge between species, which can also promote hybridization. The majority of evidence for these processes has been found between males of species that compete for mating resources, but recent evidence

suggests that female–female competition can also promote hybridization.

Competitive asymmetry and directional hybridization

Competitive asymmetry can lead to *asymmetric introgression*, in which loci and traits that confer a reproductive advantage and are inherited from a competitively superior parental species progress into the hybrid zone farther than background neutral loci (Barton 1979; Piálek and Barton 1997). For example, an asymmetry in male–male competition between 2 lineages of common wall lizards *Podarcis muralis* may be promoting directional hybridization (While et al. 2015). The lineages are divergent in competitive morphology—males of the northern Italian subspecies *Podarcis muralis nigriventris* have larger heads, stronger bite force, and greater testes mass compared with the Western Europe subspecies *Podarcis muralis brogniardii*. *Podarcis muralis nigriventris* males are more aggressive and dominant to *P.m. brogniardii* males in territorial interactions, which allows them to monopolize high-quality territories and courtship of both conspecific and heterospecific females (MacGregor et al. 2017). Sexual traits associated with *P.m. nigriventris* males, including head size and dorsal and ventral coloration, are introgressing into the hybrid zone (While et al. 2015).

Directional hybridization can occur particularly when male–male competition is a stronger determinant of mating than female mate preferences (e.g., Reichard et al. 2005). For example, in experimental secondary contact among *Tropheus* cichlid fish of different color morphs, dominance of the red male morph interfered with positive assortative mating preferences by females and promoted asymmetric hybridization (Sefc et al. 2015). When males of a dominant lineage displace lower-ranked males of the subordinate lineage from breeding territories, their conspecific females are left with no choice but to join the territory of a heterospecific in order to reproduce (Wirtz 1999). However, particularly when hybridization is maladaptive, females could still exercise choice for conspecifics through extra-pair mating with nearby conspecific males. This happens, for example, in fur seals that pursue extra-territory inseminations when their phenotype did not match that of territorial mates (Goldsworthy et al. 1999). The outcomes of interspecific male–male competition for hybridization in the *Podarcis* wall lizards may be influenced by weak female preference as well as by male mate choice for conspecifics (Heathcote et al. 2016). Although *P.m. nigriventris* males outcompete *P.m. brogniardii* males for mating opportunities in the hybrid zone, *P.m. nigriventris* males prefer to mate guard the largest females, which are typically also *P.m. nigriventris*, thereby promoting assortative mating and reducing gene flow between the 2 lineages (Heathcote et al. 2016). These examples demonstrate some of the ways competition and mate choice can interact to promote similar or opposing outcomes for hybridization. When possible, empirical studies on the behavioral mechanisms of hybridization should investigate the contributions of both male and female behavior separately, to understand the interactions between competition and mate choice (Wong and Candolin 2005).

Unidirectional hybridization resulting from competitive asymmetries can yield increased prevalence of 1 heterospecific cross—for example, mating between females of 1 species with males of the competitively dominant species, but the reciprocal cross is rare. A pattern of mitochondrial DNA (mtDNA) of only 1 parental species found in hybrids can suggest unidirectional hybridization. For example in hybridizing macaques, the Tonkean macaque (*Macaca tonkeana*) has more intense male–male competition for mates, and may be outcompeting the Moor macaque (*M. maura*) for *M. maura*

females (Supriatna 1991; Bergman and Beehner 2003). Genetic patterns of introgression for autosomal loci and mtDNA suggest that hybridization occurs between *M. tonkeana* males and *M. maura* females (Evans et al. 2001). Unidirectional introgression of mtDNA, autosomal loci, and/or phenotypic traits can be explained by sexual selection, either due to the competitive dominance of 1 species, or to mate choice favoring 1 species. It can also be found between females of a rare species and males of a common species in sympatry (Wirtz 1999). Patterns suggesting unidirectional hybridization can additionally be explained by the reduction in fitness from 1 cross type due to deleterious epistatic interactions—so-called "Darwin's Corollary to Haldane's Rule (Turelli and Moyle 2007). Studies testing whether pre-mating behaviors can explain patterns of asymmetric introgression should also consider alternative, but not necessarily mutually exclusive hypotheses of post-mating and postzygotic reproductive isolation (e.g., Carling and Brumfield 2008). For example, unidirectional hybridization between 2 sunfish species *Lepomis macrochirus* and *Lepomis gibbosus* was explained by both asymmetric conspecific sperm precedence and hybrid inviability of 1 cross (Immler et al. 2011).

Asymmetric introgression can also lead to a moving hybrid zone. Moving hybrids zones can occur between sympatric species with asymmetric competitive interactions that result in the geographic and/or genetic displacement of the inferior competitor via hybridization. Especially when an aggressive phenotype is linked with greater dispersal (Duckworth and Badyaev 2007; Canestrelli et al. 2016), range expansion of the superior competitor can cause a hybrid zone to move over time. In the *Setophaga* hybrid zone between hermit *Setophaga occidentalis* and Townsend's *S. townsendi* warblers, *S. occidentalis* are superior competitors over breeding territories and mates, and hybrids are intermediate to parentals in aggression (Pearson 2000; Owen-Ashley and Butler 2004). While hybridization is restricted to narrow zones, *S. townsendi* mtDNA is found in a phenotypically pure *S. occidentalis* population (Krosby and Rohwer 2009), and a resampling of hybrid zone sites 10–20 years later indicated they have become more *townsendi*-like over time (Krosby and Rohwer 2010). This geographic replacement of the competitively inferior *S. occidentalis* (Krosby and Rohwer 2010) could ultimately result in its extinction. Hybridization between species with asymmetric competitive abilities can have important conservation implications—resulting in the extirpation of the less competitive lineage through genetic or demographic swamping, but also facilitating genetic rescue (reviewed in Allendorf et al. 2001; Mooney and Cleland 2001; Todesco et al. 2016; vonHoldt et al. 2017). Female choice in conjunction with male–male competition can also facilitate hybrid zone movement. For example, females of both black-capped (*Poecile atricapillus*) and Carolina (*Poecile carolinensis*) chickadees display mate choice for dominant males, which are typically *P. carolinensis* (Bronson et al. 2003). The dominance of *P. carolinensis* males over territories and mates can explain its northward range expansion and the northern movement of the hybrid zone, but climate change can also explain this movement (Taylor et al. 2014). Because hybrid zone movement can be explained by many other drivers including mate choice, postzygotic genetic incompatibilities, and environmental change (Buggs 2007), hypotheses for competition as a driver of asymmetric introgression and hybrid zone movement should be explicitly tested, for example by comparing aggression to simulated territorial intrusion (e.g., Billerman and Carling 2017; Lipshutz 2017). These are not mutually exclusive processes, however, as the presence of competitive asymmetries is a

necessary but not sufficient demonstration that competition is a key driver of hybrid zone movement.

When mate choice is based on an evaluation of traits also involved in competitive interactions, it can be difficult to disentangle the effects of reproductive competition from mate choice on hybridization (e.g., Mennill et al. 2002). In the golden-collared *Manacus candei* and white-collared *Manacus vitellinus* manakin hybrid zone, male–male competition may be driving asymmetric introgression of gold plumage across the hybrid zone, as *M. candei* males are more aggressive than *M. vitellinus* males and plumage color is associated with aggression (Mcdonald et al. 2001). However, this pattern may also be driven by female preference for *M. candei* males in mixed leks (Brumfield et al. 2001; Stein and Uy 2006). As with identifying the drivers hybrid zone movement and distinguishing between ACD and RCD, we should test alternative hypothesis for competition versus mate choice in driving asymmetric introgression, for example with experimental tests of interspecific competition (While et al. 2015) and mate choice (Heathcote et al. 2016) in the same system.

Female–female competitive asymmetry
Could competitive asymmetries between females of sympatric species promote hybridization, in a similar fashion to males? Within a species, competitive phenotypes in females can influence mating success. In the social lizard *Egernia whitii*, more aggressive females have more extra-pair offspring (While et al. 2009). Between species, female–female competition for mating opportunities is less understood. Interspecific female–female competition for male sperm has been documented between mollies *Poecilia latipinna* and a unisexual species of hybrid origin *Poecilia formosa* from crossings of *P. latipinna* and *P. mexicana* (Riesch et al. 2008). In order to trigger embryogenesis, hybrid female *P. formosa* require sperm from either parental species, known as sexual parasitism (Schlupp 2009). While *P. formosa* was more aggressive toward *P. latipinna* than vice versa, it is unknown what role interspecific female competition plays in maintaining the *Poecilia* species complex (Makowicz and Schlupp 2015). That aggressive females are more promiscuous could influence their likelihood of mating with a heterospecific. Costs of heterospecific mating may be higher in females because of gametic and parental investment (Wirtz 1999), but these costs may be lowered if females mate with multiple males. For example, one experimental study of *Gryllus* crickets demonstrated that mating barriers between hybridizing species were weakest among females of the more polyandrous species (Veen et al. 2011). Females of the more polyandrous species, *Gryllus bimaculatus* discriminated less and mated more with heterospecific males. Therefore, we might expect females in polyandrous systems, especially those that compete for mates, to mate less discriminately than females in monogamous mating systems.

Interspecific female–female competition in polyandrous mating systems, in which females compete for access to male mates, may be analogous to interspecific male–male competition. Because polyandrous females have multiple opportunities to breed, they may face lower costs of heterospecific mating (Arnqvist et al. 2000). One example is a hybrid zone between 2 polyandrous sex-role reversed bird species, the wattled jacana *Jacana jacana* and the Northern jacana *Jacana spinosa* (Miller et al. 2014; Figure 2). Female jacanas of both species control access to mates by competing for territories encompassing a harem of males. Females are under stronger selection for increased aggression and larger body size and spur weaponry, while males provide parental care (Jenni and Collier 1972; Emlen and Wrege 2004a, 2004b). There is an asymmetry of

hybridization—phenotypic hybrids only had *J. spinosa* mtDNA haplotypes, suggesting predominant crosses between *J. spinosa* females and *J. jacana* males (Miller et al. 2014). Unidirectional introgression of *J. spinosa* mtDNA across the hybrid zone may be explained by interspecific female–female competition for mates, whereby the larger body size, spur length, and higher aggression of female *J. spinosa* allow them to exclude female *J. jacana* from obtaining territories in mixed-species populations (Lipshutz 2017). While interspecific female–female competition over territories and mates may be more likely to influence hybridization outcomes in species with polyandrous mating systems, to what extent does female–female competition impact the likelihood of hybridization in other mating systems?

Adaptive introgression of competitive traits
Heterospecific mating is often considered an accidental byproduct of incomplete species recognition, which reduces fitness due to wasted time, energy, and gametes. However, hybridization can also be adaptive (Willis 2013). While this review has thus far examined how competition influences the likelihood for hybridization, heterotypic mating can also increase competitive ability. For example, hybrid tadpoles between *S. bombifrons* and *S. multiplicata* develop more rapidly and are more likely to achieve metamorphosis than *S. bombifrons* tadpoles, which can facilitate survival in ephemeral ponds. *Spea bombifrons* females become more likely to hybridize with *S. multiplicata* males when water levels are low (Pfennig et al. 2002; Pfennig and Rice 2007), suggesting that unidirectional hybridization is adaptive in certain environments. Inheritance of competitive traits from the dominant parental lineage could also provide hybrids with a selective advantage over the competitively inferior lineage.

Heterosis, or hybrid vigor, occurs when hybrids are competitively superior to their parental species (Birchler 2003), and can also result in reduction or extinction of parental species. A pattern of hybrids outcompeting their parental taxa is particularly associated with invasive species (Pyšek et al. 2003; Suehs et al. 2004). Hybrids between 2 morphs of invasive Thiarid snail *Melanoides tuberculata* are produced sexually, but the hybrid morphs reproduce asexually via apomictic parthenogenesis (Samadi et al. 1999). Hybrid morphs are superior competitors to their parental taxa in natural habitats by having greater colonization ability and larger bodied offspring (Facon et al. 2005, 2008), and are mostly female (B. Facon, personal communication). There are several other examples where hybrids are superior competitors to parentals, for example in several crosses of Darwin's finches (*Geospiza* sp.) where hybrids have higher breeding success (Grant and Grant 1992), and in hybrid gulls between *Larus occidentalis* and *Larus glaucescens* because of the combination of adaptive traits from parentals in an intermediate environment (Good et al. 2000). Heterosis can also be a mechanism of speciation if hybrids are reproductively isolated from their parental species. This can occur due to an inversion (Lowry and Willis 2010) or allopolyploidy (Comai 2005; Van de Peer et al. 2017), which is more common for plants (Abbott et al. 2016) but also documented in animals (Mable et al. 2011). Heterosis can also be associated with a *hybrid swarm* because of the production of highly fit recombinant genotypes that erode parental genetic boundaries, for example in the copepod *Tigriopus californicus* (Hwang et al. 2011). In a hybrid swarm between Pecos pupfish (*Cyprinodon pecosensis*) and sheepshead minnow (*C. variegatus*), male–male competition is asymmetric (Rosenfield and Kodric-Brown 2003). Male *C. variegatus* as well as F1 hybrids outcompeted male *C. pecosensis* for mates, suggesting

hybrid vigor can promote extensive hybridization via competition. The adaptiveness of hybridization is based on the fitness of hybrids relative to parental species, and this can be challenging to quantify but useful for understanding how and why hybridization occurs. For species in which hybridization is maladaptive, introgression of traits that increase a hybrid individual's competitive advantage may be undermined by lower survival due to incompatibilities for other loci.

Convergence in agonistic signals

Although studies of interspecific competition typically focus on the evolution of trait divergence, competition over shared mating resources can actually drive convergence in signals and signal recognition involved in territorial defense to facilitate aggressive interactions between heterospecifics (Cody 1969; Tobias and Seddon 2009; Vokurková et al. 2013). Convergence in competitive signals has been found within an avian radiation of ovenbirds (Furnariidae), whereby species coexistence predicted convergence in male song (Tobias et al. 2013). Agonistic signal convergence could evolve due to direct interactions in competing over shared ecological or mating resources (Grether et al. 2009; Dufour et al. 2015; Laiolo 2017), or because of acoustic adaptation to a shared environment (e.g., Cardoso and Price 2010). Convergence in competitive signals can also occur due to hybridization (Grant et al. 2004; Secondi et al. 2011), either if signals are genetically determined and are intermediate to parental signals (e.g., de Kort et al. 2002; Gee 2005), or due to learning if offspring imprint on the songs of heterospecifics (e.g., Secondi et al. 2003; Haavie et al. 2004).

While signal convergence between sympatric species is expected to facilitate competitor recognition and interspecific territoriality (Grether et al. 2009), it could also increase the probability of heterospecific pairing and hybridization, especially in species that use the same signals to both defend territories and attract a mate (Berglund et al. 1996; Wong and Candolin 2005). For example, in sympatric *Ficedula* flycatchers, the pied flycatcher *F. hypoleuca* song converges with the song of the more dominant collared flycatcher (*F. albicollis*) by incorporating learned parts of its song repertoire (Haavie et al. 2004). This mixed singing leads to heterospecific pairing and increases the likelihood of hybridization (Qvarnström et al. 2006). However, the convergence of male song and song discrimination to facilitate territorial competition is opposed by stricter female choice in sympatry (Wheatcroft and Qvarnström 2017). These findings, that divergence in species recognition can evolve in females along with convergence in male sexual signals, provide a more inclusive understanding of reproductive isolation in the flycatcher system. This study adds to an emerging understanding that signal discrimination may diverge between the sexes, based on different selective pressures of mate and competitor recognition. In another example, a study of 2 sympatric *Hypocnemis* antbird species found that females discriminate between conspecific and heterospecific males in sympatry, despite convergence in male song (Seddon and Tobias 2010). Concerning interspecific communication in secondary contact, the evolution of signal recognition is expected to facilitate competition over a shared mating resource in males and to avoid maladaptive hybridization in females. Both convergent and divergent character displacement on the same sexual signals and their recognition can therefore have opposing outcomes for reproductive isolation in males versus females (see Box 2). When this tension exists, the selective pressures resulting divergent RCD dominate those favoring convergent ACD, due to the costs of reproduction outweighing the costs of aggression (Okamoto and Grether 2013).

When females compete, is the evolution of competitive signals and recognition in females predicted to have similar outcomes for hybridization as those found in males? For species in which both males and females defend territories, we might expect the sexes to have similar patterns of agonistic signal evolution. This can depend on whether the agonistic signals are also used in mate choice decisions for either sex (Wong and Candolin 2005). If male signals are under selection in both choice and competition contexts, but female signals are not, then we might predict fewer constraints on the direction of evolution of female signals. In a scenario where convergence in agonistic signals facilitates interspecific territorial interactions, female agonistic signals may be more likely to converge in secondary contact, whereas male signals may be expected to be more divergent to facilitate species recognition. However, if males use female agonistic signals to select a mate, then we should see similar patterns of convergence in the agonistic signals of both sexes. In a sympatric species pair of Neotropical antbirds, *Hypocnemis peruviana* and *H. subflava*, both males and females sing to defend territories, and interspecific aggression is intense (Tobias and Seddon 2009). Both male and female songs converged in sympatry, likely due to *social selection*, which includes competition for ecological resources in addition to mate acquisition (West-Eberhard 1983; Tobias et al. 2012). Interestingly, female songs showed greater similarity in acoustic structure in sympatry than male songs, potentially because of selection on male song for females to discriminate between conspecifics and heterospecifics and avoid hybridization (Searcy and Brenowitz 1988). Although hybridization does not occur between these species, this study can provide insight for female versus male agonistic signal evolution resulting from interspecific interactions. Female territorial signals may be less constrained by conspecific mate recognition than male signals, and can therefore evolve more strongly in response to interspecific competition than male signals. Currently, there are no known studies of ACD in female competitive traits and/or species recognition. Are female agonistic signals more likely to converge or diverge in secondary contact with closely related competitors, in comparison to male signals?

Conclusions and Next Steps

This review has examined the processes by which reproductive competition between species in secondary contact promotes reproductive isolation versus hybridization. When possible, I have compared the evidence for male–male competition to that of female–female competition, but thus far both theoretical and empirical studies are rare for female competition. Interspecific competition that promotes the divergence of sexual traits and/or recognition between species via character displacement, as well interspecific interactions that result in reproductive exclusion, can promote reproductive isolation (Figure 1: Conceptual framework). While evidence for ECD, RCD, and ACD includes the involvement of both males and females, reproductive exclusion has only been documented in males. Competition between species in secondary contact can also promote hybridization, for instance when a dominant species monopolizes mating resources, sometimes leading to asymmetric introgression. Convergence in sexual traits and recognition due to competition can also increase the likelihood for hybridization if the same traits are involved in mate choice. Hybridization itself can cause the introgression of competitive traits, which can facilitate further hybridization. Evidence for the involvement of both males and females has been found in all of these processes, though the male examples are strikingly more prevalent.

Our understanding of how male–male competition influences hybridization outcomes is solidifying. Still, the predictions for how female choice can reinforce reproductive isolation via selection for male trait divergence are more clearly developed than the predictions for how male–male competition can influence hybridization. This is paradoxical, because most empirical studies examining whether sexual trait divergence promotes reproductive isolation are carried out by testing male–male interactions and not male–female interactions, due to logistical challenges (see Box 2: Playback experiments). Only by testing both competition and mate choice within the same study systems can we disentangle whether the mating behavior of males and females impedes or promotes the evolution of reproductive isolation.

Does taking a non-traditional perspective change our understanding of how sexual selection impacts the process of reproductive isolation? For those systems in which females of different species compete for shared mating resources, the likelihood for female–female competition to promote reproductive isolation versus facilitate hybridization depends on the cost of mating with a heterospecific. Mating behavior is just one component of species interactions that influences the potential for hybridization between lineages in secondary contact, and the evolutionary context of interacting lineages is important to consider. The outcomes for reproductive isolation depend not only on interspecific competition and mate choice, but also the fitness costs to hybridization, which can be related to the age of divergence between the interacting lineages and accumulation of genetic incompatibilities (Pfennig 1998; Ord et al. 2011; Drury et al. 2015). For instance, the accumulation of intrinsic genetic incompatibility over time is likely to select for species recognition traits to avoid heterospecific mating. As females typically have higher gametic and parental investment and fewer opportunities for multiple mating attempts, one prediction is that male competition is more likely to result in hybridization than female competition. Future empirical and theoretical work should explicitly test this prediction on the outcome of intraspecific competition for hybridization in males versus females, in the context of the strength of intrinsic incompatibilities between sympatric lineages.

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