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The Role of Sexual Selection in Local Adaptation and Speciation

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Abstract

Sexual selection plays several intricate and complex roles in the related processes of local adaptation and speciation. In some cases sexual selection can promote these processes, but in others it can be inhibitory. We present theoretical and empirical evidence supporting these dual effects of sexual selection during local adaptation, allopatric speciation, and speciation with gene flow. Much of the empirical evidence for sexual selection promoting speciation is suggestive rather than conclusive; we present what would constitute strong evidence for sexual selection driving speciation. We conclude that although there is ample evidence that sexual selection contributes to the speciation process, it is very likely to do so only in concert with natural selection.

1. INTRODUCTION

Sexual selection has developed over the past 150 years into a multifaceted research area with a rich literature in both proximate mechanisms and evolutionary effects, which have been tackled with a wide range of theoretical, observational, and experimental techniques. On the surface, it may seem straightforward at its heart—sexual selection may cause bizarre adaptations that come with a viability cost. When thinking about sexual selection and speciation simultaneously, it is tempting to simply conclude that the former drives the latter, because of the obvious differences between species that sometimes occur in their secondary sexual characters and the fact that mate choice can cause reproductive isolation.

It is now clear, however, that the relationship between sexual selection, local adaptation, and speciation is far more nuanced. Even in its simplest form, it is a complicated process with effects that can be unintuitive. Some theoretical and empirical work shows that sexual selection can play a causal role in the speciation process (reviewed in, e.g., Kraaijeveld et al. 2011, Maan & Seehausen 2011, Panhuis et al. 2001, Ritchie 2007, Scordato et al. 2014). Even when it contributes to speciation, however, sexual selection may not have initiated the process and may not be able to complete it. Moreover, there are conditions under which sexual selection hinders rather than promotes speciation. In this review, we tie together the theoretical and empirical literature to explore the effects that sexual selection has on the ability of a species or population to adapt to its local environment, how these effects are changed when there is gene flow between populations, and how sexual selection may promote or hinder the evolution of stronger sexual isolation, resulting in speciation.

2. SETTING THE STAGE

Evolutionary biologists have not been able to establish a consensus on the effects of sexual selection on local adaptation and speciation for several reasons. Among these is that key terms critical to a clear discussion of these relationships must be carefully defined, because casual use can cause confusion. With the goal of facilitating clarity we start by establishing basic definitions and relationships between the most important terms that we use in this review.

2.1. What Is Sexual Selection?

We consider sexual selection to be an evolutionary force that leads to a change in trait frequency, arising from differences between individuals in mating success due to trait expression. By focusing on mating success instead of reproductive success, we wish to clearly separate out sexual selection from fecundity selection (including gamete limitation). Neither good genes nor the Fisher process (e.g., preference for an arbitrary trait) should be taken as the default mechanism of sexual selection; either could be involved. Although we concentrate on animals, sexual selection can occur in plants, provided that there is differential reproductive success not caused by fecundity selection.

2.2. Mate Choice Versus Preference Versus Assortative Mating Versus Sexual Selection

These are four distinct phenomena, and one should not necessarily be taken to imply the presence of the other. Mate choice is a behavioral response by which one sex selects their mate, which may be random or preferential. Preference is an underlying bias in mate choice with regard to trait phenotype; such biases may or may not lead to assortative mating or generate sexual selection. Assortative mating is the pattern that results when like mates with like. It can, but does not necessarily, result from mate choice if there are nonrandom mating preferences, but in that case it would require genetic associations between the preference and trait (e.g., females with preferences for big males would have to be large themselves). Assortative mating can also occur if, for example, different types of individuals aggregate in different microhabitats, within which random mating subsequently occurs. Thus, assortative mating does not require mate choice or the expression of mating preferences. Moreover, if all individuals across different microhabitats in the example above had equal mating success, assortative mating would not result in sexual selection.

2.3. Assortative Mating Versus Speciation

Assortative mating causes some reproductive isolation between different types in a population, because it reduces gene flow between the assortatively mating groups and is therefore key to the process of speciation by sexual selection. Assortative mating, however, may be weak, and there can be substantial gene flow even with relatively strong assortative mating. Moreover, the presence of measurable assortative mating at a snapshot of time does not imply that stronger assortative mating will evolve in the future. Populations may stall in the speciation process and maintain an intermediate level of assortative mating, or they may even reverse the process and evolve weaker assortative mating and sexual isolation (Lackey & Boughman 2017, Nosil et al. 2009). For these reasons, merely showing that some assortative mating is present is not sufficient to show that speciation is occurring. For speciation to occur by the evolution of prezygotic reproductive isolation (often termed sexual isolation), populations must move past the initial establishment of assortative mating to evolve stronger assortative mating.

2.4. Species and Mate Recognition

Assortative mating and sexual isolation may depend critically on males and females recognizing each other as potential mates. Recent claims challenge the distinction between species and mate recognition (Mendelson & Shaw 2012). However, substantial evidence suggests that these are typically not the same process. First, the recognition literature shows repeatedly that animals perceive communication signals as categorically different (e.g., Baugh et al. 2008, Nelson & Marler 1989). Abundant evidence also shows that animals recognize differences between other individuals on the basis of the categories of species, sex, age, social status, and many other attributes, rather than placing signals or individuals on a continuum with no boundaries (e.g., Bradbury & Vehrencamp 1998, Sherman et al. 1997). Second, conflating mate and species recognition ignores important cognitive aspects of mate choice. Several studies demonstrate complex decision-making by females that makes use of this information by showing they do not merely respond to a continuum of trait values (e.g., Cummings 2015). Moreover, data show that females use different decision rules when evaluating males of their own or another species, arguing strongly against the idea that females ignore species identity (Kozak et al. 2009, 2013).

Nonetheless, early in speciation mate recognition can be an important factor initiating the evolution of reproductive isolation (e.g., Dopman et al. 2010, Lackey & Boughman 2017, Matsubayashi & Katakura 2009, Mendelson 2003, Merrill et al. 2011). Empirical studies often focus on intermediate and later stages of speciation, after measurable reproductive isolation has evolved. In contrast, the early stages of the speciation process are most commonly considered in theoretical studies, which often assume single traits are involved in the diversification process. Thus, mate recognition traits may become species recognition traits in time, although this is not necessarily so. Given this disconnect between the theoretical and empirical literatures, we are specific about species or mate recognition when we discuss the empirical literature in particular.

As we show below, the relationships between sexual selection, local adaptation, and speciation can be surprisingly complex and unintuitive and have not yet been completely determined. Moreover, researchers using different techniques, especially theoretical versus empirical techniques, have tackled the problem from widely different perspectives that seem to have little intersection (M. Kopp, M.R. Servedio, T.C. Mendelson, R.J. Safran, R.L. Rodríguez, et al., submitted manuscript). We point out areas where this is especially true in our review. What constitutes an important theoretical advance or problem may not jive with what makes an important empirical advance or problem; therefore, we do not advocate that one be forced into the structure of the other. We hope, however, that by combining theoretical and empirical perspectives in this review, we can facilitate better dialogue and more progress. Some questions are more readily addressed by theory, whereas for others more headway can be made through empirical approaches.

3. PROVING A CAUSAL ROLE FOR SEXUAL SELECTION IN SPECIATION

Much of the evidence currently in the literature provides indirect support for sexual selection playing a causal role in speciation, suggesting but not directly demonstrating its role (Rolán-Alvarez & Caballero 2000). Almost no empirical evidence demonstrates that sexual selection is the sole cause. Evidence for sexual selection's role often includes the straightforward finding that male mating traits differ among populations, that sexual traits differ among populations more than ecological traits, or that the mating rate among heterospecifics is low compared with the rate among conspecifics (i.e., sexual isolation is present) (e.g., Arnegard et al. 2010, Kaneshiro 1988, Mendelson & Shaw 2005). All of these findings are consistent with, but do not directly test, the hypothesis that sexual selection causes speciation.

The need for strong and direct evidence can be shown by a thought experiment: Imagine that owing to differences in the environment in two regions connected by gene flow, divergent selection acts on a trait such that the optima with regard to viability selection are far apart. Imagine also that this trait is subject to sexual selection, but the population preferences are not as diverged as the trait optima (in Section 5.1, we discuss when this would be expected to occur). Theoretical models show that stronger sexual selection in this scenario can pull trait means closer together instead of pushing them apart (**Figure 1**) (e.g., Lande 1982, Servedio & Bürger 2014). A snapshot

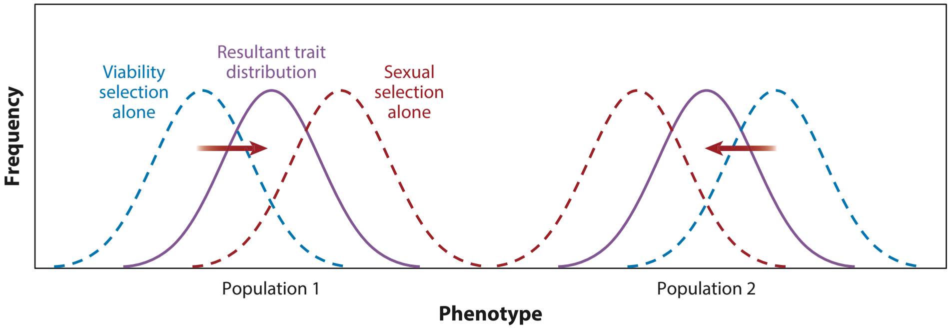

Figure 1

Conditions under which divergent preferences can still erode trait divergence. If the viability fitness distributions for traits across two populations (*blue dashed curves*) are more divergent than the distributions of preferred traits (*red dashed curves*), then sexual selection will oppose trait divergence (*red arrows*). The resultant trait phenotype distributions (*purple solid curves*) are closer together than they would otherwise have been through viability selection alone.

in time will reveal matching divergent preferences and traits—mate choice will contribute to reproductive isolation. Yet, it cannot be argued in this scenario that sexual selection per se caused the trait divergence or reproductive isolation.

Direct, strong empirical evidence that sexual selection plays a causal role in speciation is hard to come by. The gold standard for such evidence should include an experimental manipulation to test that the mechanism promoting divergence actually is sexual selection, not natural selection. This could be shown if female preferences have evolved some differentiation and clearly generate divergent sexual selection (above and beyond viability selection on the trait; see **Figure 1**), if male mating traits differ under the action of sexual selection (either female choice or male competition), and if female preferences and/or male mating traits are directly tied to increases in reproductive isolation. Showing the key importance of premating isolation to overall reproductive isolation is also strong evidence (Lackey & Boughman 2017) when coupled with data that show sexual selection causes much of the premating isolation (Boughman 2001, 2007; Keagy et al. 2016; Oh & Shaw 2013; Seehausen et al. 2008).

Importantly, even with the kind of strong evidence suggested above, sexual selection that is currently promoting divergence may not continue to increase reproductive isolation in the future. The evolution of strong from weak reproductive isolation is a complex process that can involve the evolution of choosiness, not just preference means, and as we discuss below it is tricky to empirically test whether sexual selection causes choosiness to evolve. To credit sexual selection with a causal role in speciation from observations at a snapshot in time is thus problematic. To get around these challenges, studies can compare the effects of sexual selection in populations at different stages of divergence and speciation, across the speciation continuum (Lackey & Boughman 2017). Other approaches use the power of evolutionary replication by comparing multiple populations and testing for parallel evolution of sexual isolation (Allender et al. 2011; Boughman et al. 2005).

Another factor to consider is that strong preferences are more likely than weak preferences to cause more evolutionary change in male traits, with some exceptions discussed elsewhere in this review (see Section 5.1). However, the key for speciation is whether mate preferences differ between populations, because this should cause the greatest divergence in male mating traits (Rodríguez et al. 2013). Such divergence in both preference and trait are expected to reduce mating between populations and increase sexual isolation (Boughman 2001). The importance of divergent over strong sexual selection may seem obvious, but most comparative studies consider only proxies for the strength of sexual selection, such as extent of dimorphism, and do not test the influence of divergent sexual selection. Equivocal results from such comparative studies (Panhuis et al. 2001) may in part be due to this discrepancy.

In the following sections, we discuss three types of evidence for the role of sexual selection in speciation: evidence suggesting its involvement; strong evidence that it plays a causal role; and, in our conclusion, evidence it is the sole cause of speciation. First, we turn to allopatry, in which the effects of sexual selection are not complicated by gene flow. Many of these effects also exist with gene flow, although we do not reiterate these in the later sections of this review. We refer the reader to **Table 1** as a companion guide and summary of the main effects of sexual selection described in the text.

4. SEXUAL SELECTION, LOCAL ADAPTATION, AND SPECIATION IN ALLOPATRY

Local adaptation within a single population presents many interesting theoretical and empirical questions, as environmental optima may fluctuate and change, and drift, mutation, and genetic constraints may make such optima difficult to reach. Although it is beyond the scope of our review

Table 1 A summary of the primary effects that sexual selection (SS) will have on local adaptation and speciation and the likely cause[a]

Situation	Source of SS	Primary effects of SS
Local adaptation in single population	Preference for arbitrary traits	SS counters viability selection, reducing local adaptation
	Preference for condition-dependent traits	SS purges deleterious mutations, facilitating local adaptation
	Preference for locally adapted traits	SS facilitates local adaptation
Allopatric speciation	Preference for trait off its optimum	SS moves the population to a new adaptive peak The population can drift along a line of preference/trait equilibria The population can settle on different peaks in a multipeak landscape (mutation order)
Speciation with gene flow	Neutral absolute preference	Preferences will tend to homogenize Preference homogenization hinders sympatric divergence and reduces trait differentiation between geographically isolated populations
	Neutral open-ended or relative preference	Preferences will tend to homogenize but can still promote trait divergence
	For neutral absolute, open-ended, or relative preferences	Asymmetric preferences lead to trait loss
	Preference for single condition-dependent trait that indicates locally adapted males	Even with a uniform preference, SS promotes trait divergence to locally adapted optima
	Selected and locally adapted preferences	Preferences diverge easily, promoting trait divergence
	Selected preference for context-dependent benefits	Preference may diverge when ecology differs, promoting trait divergence
	Preference for trait possessed by female herself (phenotype matching)	Preference homogenization does not occur There is positive frequency-dependent SS with variable effects depending on geography and the initial trait distribution

[a] This information should be seen as a starting point. As the main text emphasizes repeatedly, the actual effects of SS can be nuanced. Therefore, we caution readers to consider complicating factors. We refer readers to the main text for details and references for each of these effects. In all of the scenarios indicated, sexual conflict is likely to reduce adaptation to local conditions and to novel peaks.

to cover these points in detail, we acknowledge that even in a situation with no gene flow from other populations, and absent sexual selection, local adaptation is not entirely straightforward. We concentrate in this section on two issues that focus on the effect of sexual selection on this process in strict allopatry: (*a*) how local adaptation is affected by sexual selection within a single population, and (*b*) how sexual selection affects whether allopatric populations can evolve reproductive isolation.

4.1. Adaptation with Sexual Selection in a Single Population

Adaptation is generally considered with reference to viability selection applied by both the local abiotic and biotic environments (the same ideas apply to fecundity selection). Logically, the main effect of sexual selection will be to push a population off of an optimum determined by viability selection (e.g., Kirkpatrick 1982, Lande 1981). The only way that sexual selection can improve the fitness of a population with regard to a locally adapted optimum is if it can increase the rate or probability that this optimum is reached or decrease the variance of the population around this optimum.

A number of theoretical models have outlined mechanisms by which sexual selection can increase fitness in this way. Lorch et al. (2003) point out that these mechanisms presuppose that females prefer males with the highest condition. When mating traits are condition dependent, sexual selection is likely to act on many loci across the genome through a process known as genic capture (Rowe & Houle 1996). This process occurs when mutations reduce viability and/or sexual fitness, and hence, condition. Sexual selection for condition can thus purge deleterious mutations from a population, in turn reducing mutation load and potentially drift load, increasing beneficial variants, and potentially preventing extinction (Agrawal 2001, Lorch et al. 2003, Siller 2001, Whitlock 2000, Whitlock & Agrawal 2009). Condition dependence can also lead to a mating advantage for locally adapted males, which can allow niche expansion and increase successful colonization of new areas (Proulx 1999, 2002).

These predictions have been tested with experimental evolution studies. Sexual selection can help purge maladaptive alleles (Hollis et al. 2009). These effects of sexual selection may be especially pronounced in harsh environments, which is likely when populations are far from the optimum. However, sexual selection does not always improve adaptation (Arbuthnott & Rundle 2012, Hollis & Houle 2011), primarily because the benefits of sexual selection removing deleterious alleles are countered by the costs arising from sexual conflict. Sexual conflict occurs when fitness optima differ for the sexes, generating antagonistic selection, and the costs of conflict can pull populations off their fitness peak. These contrasting results suggest that the magnitude of the benefits of sexual selection relative to costly sexual conflict determines whether adaptation is helped or hindered (see also Fricke & Arnqvist 2007). Much of this work has been done in *Drosophila*, in which sexual conflict is strong. More work on systems that may vary in the strength of sexual selection versus sexual conflict is warranted to determine whether this counterbalancing is fairly general or limited to certain kinds of systems. Additionally, theoretical studies are needed that incorporate sexual conflict into the effects of sexual selection on fitness, mutation load, genetic load, and extinction risk.

Empirical work also shows that sexual selection can affect not only diversification but also extinction. A few recent empirical tests show that condition-dependent purging can guard against extinction in novel environments even under inbreeding (e.g., Lumley et al. 2015), consistent with theoretical predictions (Whitlock 2000, Whitlock & Agrawal 2009). Lumley and colleagues (2015) showed that selection lines that experienced strong sexual selection maintained high fitness and avoided extinction for twice as long as lines that experienced weak sexual selection. The way that sexual selection influences extinction is also important in the larger context of overall diversification, and some theoretical and comparative studies suggest it increases extinction risk rather than decreasing it (e.g., through drastic decreases in male viability or population fitness) (Doherty et al. 2003, Houle & Kondrashov 2002, Kokko & Brooks 2003), arguing for further work on these questions.

4.2. Local Adaptation with Sexual Selection Can Drive Allopatric Speciation

We turn now to how these processes affect speciation and the buildup of reproductive isolation. As discussed above, one effect of sexual selection can be to displace a population from a viability optimum. While this at least temporarily reduces adaptation in a single population, there are several ways this can lead to divergence between allopatric populations and potentially reproductive isolation. First, movement of a population away from one peak can lead it into the basin of attraction of another peak (Bonduriansky 2011). Movement between peaks in an isolated area could facilitate ecological divergence between the novel and original populations. This mechanism complements the possibility that the presence of a new peak in a novel environment can itself lead to successful colonization if local adaptation is reflected by condition dependence (Proulx 1999, 2002). Sexual selection can also lead to a range of high-fitness phenotypes determined by a combination of viability and sexual selection, whereby populations in geographically separated areas can evolve different preference and trait genotypes owing to genetic drift (Lande 1981). This process can lead to reproductive isolation when preferences are either neutral or costly (e.g., Uyeda et al. 2009). Finally, a process akin to mutation-order speciation (e.g., Mani & Clarke 1990) can occur with sexually selected traits, whereby different populations may evolve to different sexually selected optima when initial preference landscapes have multiple peaks (Mendelson et al. 2014). We discuss differences between populations in preference optima caused by viability selection in Section 5 below.

Several experimental evolution studies show that sexual selection facilitates divergent adaptation to novel environments in the absence of gene flow. For example, Fricke & Arnqvist (2007) conducted a nice experimental evolution test of the dual contributions of natural and sexual selection. They show that sexual selection complements natural selection on a novel host, increasing local adaptation of host acceptance and larval performance while opposing natural selection on the ancestral host, in which the combined effects of sexual and natural selection lead to stabilizing selection (Fricke & Arnqvist 2007). These effects could increase divergence because the population on the novel host is more likely to reach the novel peak, whereas the ancestral population is constrained to its ancestral peak. Contrasting evidence shows that sexual selection can hinder adaptation to a novel peak partly owing to sexual conflict (Almbro & Simmons 2013, Reding et al. 2013). In general, changing environments may alter the benefits of sexual selection and costs of conflict. Sexual selection might most effectively aid adaptation in a novel environment where the population is likely to be far from the new optimum. Conversely, sexual conflict may prevent populations from reaching fitness peaks because of the costs each sex experiences, which may erode population fitness.

We now consider how sexual selection affects speciation in allopatry, which has been explored with experimental evolution in several study systems, including *Drosophila* (e.g., Rundle et al. 2005) and yeast (e.g., Greig 2009). In the *Drosophila* studies, however, changes occurred in parallel with environment, so either sexual selection or natural selection may have been the cause of trait or preference divergence. A later experiment manipulated both forms of selection and found corresponding responses, indicating that sexual selection plays a role and could cause divergence on its own. However, the joint action of natural and sexual selection caused more divergence than either alone (Rundle et al. 2009). Another experiment with *Drosophila* manipulated the opportunity for sexual selection alone and found divergence in both male song and female preference for song leading to divergent species recognition (Debelle et al. 2014). Unlike many other experiments, female preference divergence exceeded male trait divergence, suggesting that female preferences could have caused the divergence in male traits.

In a number of natural systems, differentiation in mating traits seems to occur in allopatry, most noticeably in male mating traits but sometimes also in female preferences. For example, in Laupala crickets, male courtship song differs among species in temporal characteristics and females appear to differ in preference (e.g., Oh et al. 2012). However, the cause of this differentiation and the precise role sexual selection plays are not clear, in particular for female preferences, so more work is required on the mechanisms. In other systems, the differentiation that occurs in allopatry is revealed upon secondary contact or in hybrid zones (While et al. 2015), which often gives high power for revealing the underlying role of sexual selection.

Many of the empirical studies above were not designed to directly consider the effects of gene flow, which poses unique challenges for the evolution and maintenance of differentiation. When there is gene flow, how often do naturally and sexually selected traits diverge together, and what conditions are necessary for this to occur? We discuss these questions in more detail next.

5. LOCAL ADAPTATION AND SPECIATION WITH GENE FLOW

The problem that gene flow poses for the evolution of trait differentiation, and ultimately reproductive isolation, is closely related to the problem that it poses for adaptation in general. Gene flow opposes local adaptation by bringing maladapted migrants into a population, and when mating is random, the influx of migrants prohibits a population from remaining at a natural selection optimum. Thus, when there is strong divergent ecological selection, trait differentiation that occurs within one generation will be at least partially negated if migration and random mating with subsequent recombination takes place (e.g., Felsenstein 1981). This problem can be mitigated by the evolution of assortative mating. Adaptive assortative mating mechanisms can, however, be opposed by gene flow, in an analogous fashion to locally adapted traits. In this section, we discuss in more detail specific aspects of the difficulties raised by gene flow and their possible solutions. We stress throughout whether sexual selection is expected to promote or inhibit trait divergence and the evolution of sexual isolation, and we summarize these effects in **Figure 2**.

5.1. Population Divergence with Neutral Preferences

The effect of sexual selection on the divergence of locally adapted traits is dependent on whether or not population-specific preferences for specific traits can maintain differentiation across incipient species. We start by considering the situation in which preferences are not themselves under direct divergent selection, such as in a strictly Fisherian process (neutral preferences). When preferences and traits are under separate genetic control, sexual isolation occurs when preference and trait distributions diverge to the point of no overlap between species (including by the evolution of very strong choosiness). Yet, theoretical studies demonstrate that when reproductive isolation relies on different preferences to predominate in each incipient species, gene flow can cause preferences to partly or completely homogenize (Servedio & Bürger 2014, Weissing et al. 2011). This can prevent preference differentiation in sympatry, which already presents a worst-case scenario for the evolution of reproductive isolation (van Doorn et al. 2004, Weissing et al. 2011). It can also reduce preference differentiation in what initially seems like a best-case scenario, one in which preference and trait have already diverged in allopatry and migrants connect populations that otherwise remain spatially separated (Servedio & Bürger 2014, 2015).

The sexual selection generated by these partly or completely homogenized preferences will in turn tend to homogenize sexually selected traits. This prevents selectively neutral traits from maintaining differentiation along a cline or with spatial separation (e.g., Lande 1982, Payne & Krakauer 1997, Servedio & Bürger 2014). Even when mating traits themselves are locally adapted, homogenizing sexual selection will still tend to erode trait differentiation by drawing together trait frequencies off of migration/selection balance as shown in **Figure 1** (Lande 1982, Servedio & Bürger 2014). Additional selective forces, such as selection against hybrids during the process of reinforcement (Dobzhansky 1937), can promote both preference and trait divergence to some extent, but preference divergence is still relatively difficult to obtain (e.g., Kirkpatrick & Servedio 1999, Servedio 2004, Servedio & Kirkpatrick 1997).

The tendency for reduced preference differentiation to lead to similarly reduced trait differentiation especially holds for absolute preferences, defined as preferences for a specific trait value (**Figure 2**). Absolute preferences are found to reduce trait differentiation along a cline in quantitative genetic models (Lande 1982). Population genetic models with separate preference and

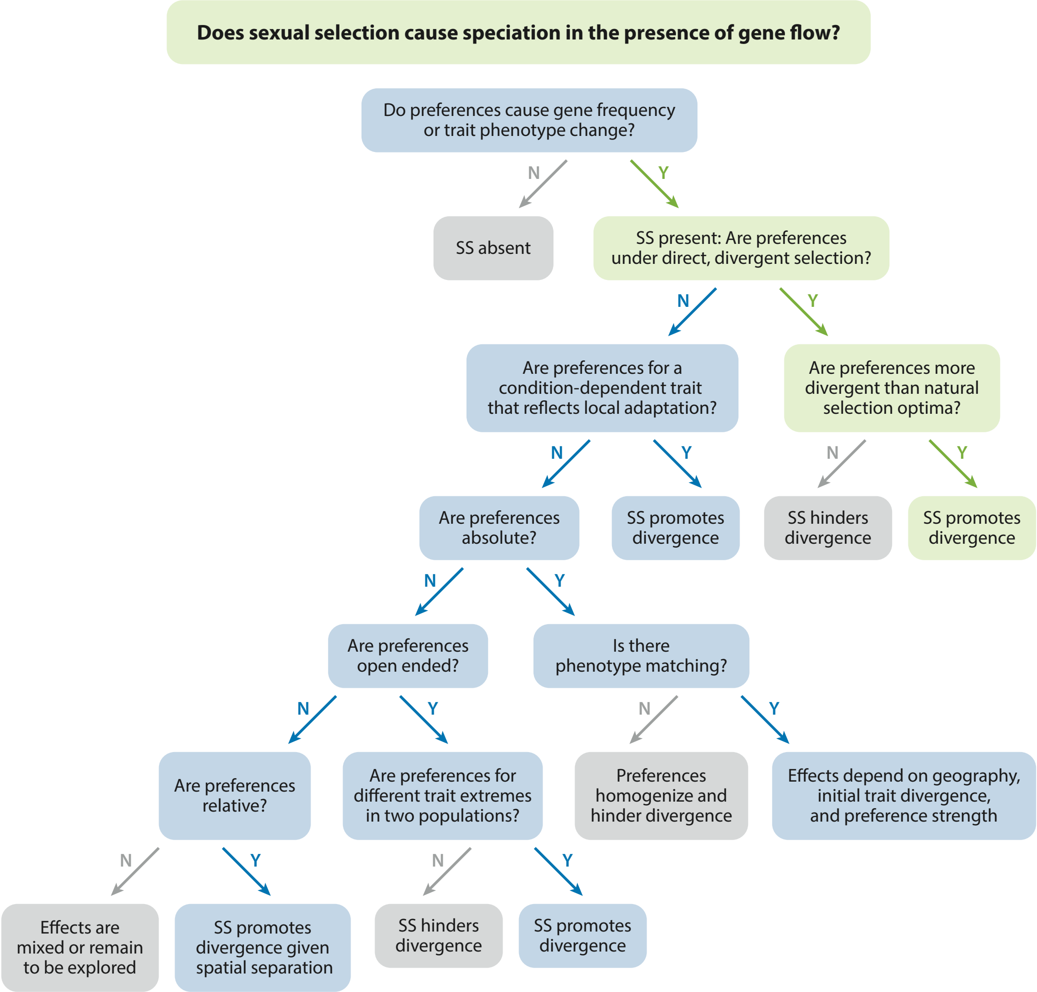

Figure 2

This decision tree can be used to evaluate the likely effect of sexual selection via female preference on speciation with gene flow under many of the scenarios we consider in this review. When sexual selection promotes divergence, we infer that sexual isolation will increase. For simplicity, this figure does not consider the joint effects of natural selection. The most straightforward path to speciation is at the far right of the figure, highlighted in green. Other paths in which sexual selection promotes speciation are highlighted in blue. Outcomes in which sexual selection hinders speciation are highlighted in gray. Abbreviations: N, no; SS, sexual selection; Y, yes.

trait loci behave analogously to absolute preferences in this respect (Servedio & Bürger 2014, 2015). There are other preference functions, however, for which even a large degree of preference homogenization across incipient species does not necessarily homogenize traits (**Figure 2**). Lande (1982) also studied preferences for traits that are offset from the population mean trait phenotype after viability selection by a certain amount (relative preferences). Logically, in this case any tendency for preferences to differ between populations in the direction of that offset will cause traits to diverge in opposite directions from their value before mating. Indeed Lande (1982) found such preferences to always amplify trait differentiation along a cline. Preferences for extreme values (open-ended or psychophysical) should likewise select for divergence provided there is even the smallest amount of preference divergence between populations; Lande (1982) shows that such preferences also enhance trait divergence (note that asymmetries can still lead to trait loss; see Arnegard & Kondrashov 2004). Yet another preference rule, best-of-n, in which the choosing sex mates with the most appealing mate from a set sample size, can in some cases lead to a nonmonotonic relationship between the strength of preference and trait divergence (Servedio & Bürger 2014). The preference function or rule operating in a species is thus critical in determining the ultimate effect of preference evolution on divergence in locally adapted traits.

Whether preference functions are open ended or absolute (aka, unimodal, similar to absolute) varies by taxa, with many showing open-ended preferences (stickleback fish: Boughman 2001, Head et al. 2013; wolf spiders: Hebets & Maddison 2005) whereas others show unimodal preferences (treehoppers: Rodríguez et al. 2006). The shape of preference may influence whether isolation results from mate choice and whether isolation is symmetric (Ritchie 1996). However, further details on the shape of preference functions are difficult to determine empirically. Therefore, rather than measure the shape of individual preference functions, much work related to the type of choice has focused on search rules, otherwise known as mate sampling strategies. Many of these studies have determined that females use decision rules in evaluating males that reflect absolute preference because female preference is not influenced by the suite of males available but reflects an internal and bounded standard (e.g., Brandt et al. 2005, Leonard & Hedrick 2009). Other studies show that a best-of-n strategy is used and is influenced by experience and reproductive success from prior matings (e.g., Uy et al. 2001). More theoretical and empirical work needs to be done on these questions before firmer conclusions can be drawn about which taxa and preference rules are more or less likely to foster speciation.

5.1.1. Condition dependence and local adaptation. An interesting mechanism of mate choice that circumvents the problem of gene flow homogenizing mating preferences has been developed from an idea initially suggested by Proulx (1999, 2001, 2002). When only locally adapted males are able to express a condition-dependent signal, a preference for such signals can evolve across multiple populations without being countered by migration or recombination; the offspring of such females would tend to carry the locally successful allele, and there would be no variation in preference between populations (the preference would always be for the condition-dependent trait, but the males capable of producing this trait would differ between locations; Proulx 2001). This phenomenon, termed "locally adapted male mating advantage" (Proulx 1999), can result in the evolution of female choice with simultaneous trait divergence (Proulx 2001). The interpretation of this model was extended to encompass population differentiation and speciation (**Figure 2**) by Reinhold (2004) and by van Doorn et al. (2009), the latter of which also considered the coevolution of costly male signal, as well as by Proulx & Servedio (2009), who compared preference evolution during reinforcement under various strategies of this type. Further studies have confirmed the feasibility of this mechanism with other preference functions, alternate forms of costs (including on preferences), and condition-dependent expression of preferences in females (Schindler et al. 2013, Veen & Otto 2015).

Abundant empirical evidence shows that sexual traits are condition dependent, more so than ecological traits (e.g., Bonduriansky & Rowe 2005, Boughman 2007). Studies also show that the condition dependence of sexual traits varies with environment (Giery & Layman 2015, Vergara et al. 2012), possibly owing to allocation tradeoffs or different costs and benefits of expression. Most importantly for speciation, the extent of condition dependence correlates with the strength of preference and the magnitude of sexual isolation (Boughman 2007), suggesting that choosiness has evolved.

5.2. Population Divergence with Selected Preferences

Direct selection on preferences can greatly promote speciation (**Figure 2**) (Maan & Seehausen 2012, Servedio et al. 2011). Ultimately, such selection can increase preference variation relative to trait variation in a population. During sympatric speciation, for example, speciation can be promoted because preference variance must be greater than trait variance to establish the competitive conditions among mates that cause evolutionary branching of mating traits (van Doorn & Weissing 2001, van Doorn et al. 2001, Weissing et al. 2011). Such selection on preferences can occur through several mechanisms, the most well-studied of which is sensory drive.

5.2.1. Sensory drive.

Female preferences can become locally adapted through a process known as sensory drive (Endler 1992), in which communication systems evolve in response to prevailing environmental conditions, often termed the signaling environment because of how it affects the transmission and detection of communication signals. Differences in the signaling environment can cause coevolutionary change in three ways: (*a*) in sensory systems, (*b*) in female preferences, and (*c*) in signaling traits including male mating traits. Sensory drive is general to all communications systems; however, in this section we focus on how divergence in sensory tuning affects sexual communication. When environments differ, senses, preferences, and signals can diverge.

1. Sensory systems adapt to environmental properties influencing how well predators, prey, and social partners can be detected and discriminated (e.g., Ryan & Cummings 2013). The signaling environment influences which sensory modality dominates (i.e., vision, hearing, olfaction, or touch; e.g., Soares & Niemiller 2013) and how sensory systems are tuned (i.e., the system's sensitivity to different sound frequencies, light wavelengths, or odors; Bradbury & Vehrencamp 1998). For example, depending on light environment, species of surfperch differ in reliance on color or brightness contrast for object detection (Cummings 2007). In turn, sensory differences affect signal and preference evolution because mating signals enhance detectability of mates by matching these sensory biases of the visual system (Cummings 2007).
2. Divergence in mate preference can occur as a pleiotropic effect of sensory system adaptation to environments that differ in properties influencing detection and discrimination. For example, preferences can also be directly selected because preferring highly detectable signals can reduce the costs of choice by decreasing search time or facilitating comparison (Boughman 2002, Dawkins & Guilford 1996). This can lead to divergent selection on preferences when environments differ.
3. As female preferences differentiate, they can generate divergent sexual selection on male mating signals, causing the latter to diverge (Boughman 2001, Fuller et al. 2005, Martín & López 2008, Rafferty & Boughman 2006, Rodd et al. 2002). Several studies show that male signals closely match the sensory tuning of females (Ryan & Rand 1993, Wilczynski et al. 2001) and their divergent preferences (Rodríguez et al. 2013). Sensory drive promotes speciation when female preferences in one population do not match male signals in another, causing divergent mate and species recognition leading to sexual isolation (Boughman 2002). This joint response of senses, preferences, and signals to environmental differences induces sexual isolation.

Because the process depends on environmental differences to cause differentiation of sensory systems, female preference, and male traits, sensory drive is likely to contribute to speciation only when populations inhabit different environments. Therefore, it is most likely in allopatry or parapatry but is also possible if individuals sort into distinct microhabitats in sympatry or populate a gradient across a continuous habitat (e.g., Kawata et al. 2007). This can occur because ecological specialists occupy different signaling environments (Boughman 2001, Leal & Fleishman 2004, Seehausen et al. 2008) or when habitat choice depends on phenotype (Boughman 2002, Edelaar et al. 2008, Ravigné et al. 2009). Sensory drive can also contribute to speciation in a secondary contact situation. When gene flow is possible, sensory drive will be facilitated by strong divergent selection and by either pleiotropy or linkage of genes for perception, preference, and signals (e.g., Wiley et al. 2012). Moreover, sensory drive that involves multiple modalities (e.g., visual, olfactory, mechanosensory), such as seen in sticklebacks (Rafferty & Boughman 2006), can cause greater overall divergence and reproductive isolation.

Sensory drive is largely, but not exclusively (e.g., Kawata et al. 2007), an empirical area of study. In part, this is because direct selection is known to be stronger than indirect selection (e.g., Kirkpatrick & Barton 1997), rendering the effects of direct selection (e.g., via sensory drive) on preferences relatively easy to understand theoretically (e.g., Servedio 2001).

5.2.2. Context-dependent benefits of mate choice. Preference evolution can be influenced by ecological conditions; this concept has been termed context-dependent benefits of choice. Empirical findings suggest that the ecological context of mating interactions influences sexual selection by altering the benefits and costs of mate choice, potentially for both direct and indirect benefits (Cornwallis & Uller 2010, Jia & Greenfield 1997, Welch 2003). For example, when density is high, females who prefer and choose large males may indirectly benefit by their offspring inheriting the alleles for large size, which can help in competitive interactions; however, when food is scarce, such preference may be costly because large offspring require more food and are more likely to starve. Thus, context-dependent selection can act on preference, potentially causing it to evolve. Ecological context can also influence the traits that determine success in male competition (Lackey & Boughman 2013a), showing that both aspects of sexual selection can be affected. Thus, ecology influences the direction and extent of preference and male mating trait evolution within populations. Moreover, if populations inhabit consistently different environments, there may be consistent differences in the direction and intensity of sexual selection, which can cause divergence in both preferences and traits between populations. Either different values of the same trait can be favored or different traits can be targeted by sexual selection. On secondary contact, either can lead to reproductive isolation among populations that evolved in different environments.

Context-dependent sexual selection has been studied with long-term data sets. For example, Robinson and colleagues (2012) found that female flycatchers benefit from choosing ornamented males only in dry years (favorable ecological conditions), arguing context dependence could cause divergence for populations in different environments and could provide stasis for populations that experience variable environments. Others have used reciprocal transplant experiments to show that the indirect benefits of mate choice depend on environment in multiple taxa, including moths, frogs, and fish (Jia & Greenfield 1997, Welch 2003). Although theoretical work is inclined to separate direct from indirect selection, the focus of empirical work has been on the environmental dependence of selection and recognizes that both direct and indirect selection on preference may depend on ecology.

5.2.3. Phenotype matching. In some cases, sexual selection can lead to trait differentiation without phenotypic preferences that are distinct from trait identity. This occurs, for example, when assortative mating is a result of phenotype matching, whereby females base their preference on the trait that they themselves carry. Speciation can consequently result from either the divergence of trait distributions until they do not overlap or the evolution of very strong choosiness. The theoretical properties of phenotype matching are relatively well understood, as it is very commonly assumed in speciation models (e.g., Bolnick 2004, Bürger & Schneider 2006, Dieckmann &

Doebeli 1999, Gourbiere 2004, Kirkpatrick 2000, Kirkpatrick & Nuismer 2004, Matessi et al. 2001, Otto et al. 2008, Pennings et al. 2008, Rettelbach et al. 2013, Servedio 2004). Phenotype matching can occur by a variety of behavioral mechanisms (reviewed in M. Kopp, M.R. Servedio, T.C. Mendelson, R.J. Safran, R.L. Rodríguez, et al., submitted manuscript), including self-reference, and certain forms of mechanical compatibility (e.g., chirality in snails). Under phenotype matching, any evolutionary force that promotes differentiation of the trait will also, by definition, lead to differentiation of the preference (as the preference and trait are effectively one and the same). Because of this property, preferences cannot homogenize independently of the trait, and the attendant loss of trait divergence by sexual selection cannot occur.

Phenotype matching causes sexual selection to be positive frequency-dependent, on the basis of the frequency of the trait itself. During sympatric speciation, such sexual selection can be stabilizing if initial trait distributions are unimodal and can oppose divergent ecological selection (e.g., Matessi et al. 2001, Otto et al. 2008, Pennings et al. 2008). When traits have skewed distributions, this positive frequency-dependent sexual selection can instead be largely directional, potentially eliminating trait variation upon which the evolution of reproductive isolation rests (e.g., Bürger & Schneider 2006, Bürger et al. 2006, Norvaišas & Kisdi 2012, Otto et al. 2008, Pennings et al. 2008). In both the case in which it is stabilizing and the case in which it is directional, sexual selection thus retards the process of divergence. In contrast, when substantial trait divergence or a bimodal trait already exists, as may occur when there is secondary sympatry, positive frequency-dependent sexual selection can be disruptive and hence promote further trait divergence (Otto et al. 2008). Furthermore, under some secondary contact conditions, this disruptive sexual selection can maintain trait divergence even without ecological selection on the trait (Kirkpatrick 2000, Servedio 2011).

Interestingly, under phenotype matching, stronger and stronger preferences will eventually eliminate frequency-dependent sexual selection in a population. To understand this, consider the extreme case in which females mate only with preferred males and the frequencies of trait phenotypes are the same in both sexes. Under these conditions, all males will have equal mating success, because rare and common males will gain mates in proportion to their frequencies, causing strong assortative mating but minimal to no sexual selection. Consequently, sexual selection from phenotype matching induces the strongest divergent sexual selection between populations when preferences are intermediate in strength (e.g., Cotto & Servedio 2017, Servedio 2011, Servedio & Bürger 2015), even during the process of reinforcement (Proulx & Servedio 2009, Servedio 2004).

Many theoretical models assume phenotype matching partly as a simplifying assumption; however, empirical work has not yet determined whether it is common or rare (reviewed in M. Kopp, M.R. Servedio, T.C. Mendelson, R.J. Safran, R.L. Rodríguez, et al., submitted manuscript). One way to empirically test for phenotype matching is with behavioral data on preference and trait pleiotropy, which is a mechanism of phenotype matching because the preference depends on the trait. For example, sticklebacks have been shown by a manipulative experiment to mate assortatively by body size, suggesting phenotype matching (McKinnon et al. 2004), although mate preference divergence may also be contributing (Head et al. 2013). Even if behavioral tests indicate that preference is separate from trait, the same locus or loci may control preference and trait. Evidence of pleiotropy in a speciation context is provided by preference and quantitative trait loci (QTL) colocalizing to the same region (e.g., Kronforst et al. 2006, Wiley et al. 2012). This finding could, however, indicate that preferences and traits have independent genetic loci that are closely linked, and distinguishing these possibilities requires further work.

Theoretical studies show that phenotype matching can be closely mimicked in its evolutionary properties by sexual imprinting on parental phenotypes (Verzijden et al. 2005, 2012), even though imprinting relies on a different biological process than does phenotype matching. For example, imprinting may be on traits not expressed in the choosing sex or may occur when sexes differ in trait values. As long as the trait imprinted upon differs between species (most likely with locally adapted traits), mate recognition based on imprinting will lead to assortative mating and turn mate recognition into species recognition. The effect of imprinting on speciation is challenging to test empirically but has been shown in several systems (Cate & Vos 1999, Kozak et al. 2011, Slagsvold 2006, Verzijden & Cate 2007).

6. EVOLUTION OF STRONGER CHOOSINESS

To understand how sexual selection affects speciation, we ultimately need to know how it affects the evolution of stronger reproductive isolation. Theoretical models have primarily approached this by considering increased choosiness, defined here as strength of preference. One way that choosiness can be affected by sexual selection is through cascading effects of sexual selection on trait divergence (i.e., indirect selection on choosiness from selection on the trait). With phenotype matching, these effects are quite context dependent. As explained above, during sympatric speciation, positive frequency dependence can generate either stabilizing or directional sexual selection (the latter of which can cause trait loss). Both effects can cause intermediate choosiness to evolve (e.g., Bürger & Schneider 2006, Bürger et al. 2006, Matessi et al. 2001, Otto et al. 2008, Pennings et al. 2008). In contrast, in secondary sympatry, when trait distributions are bimodal, positive frequency-dependent sexual selection from phenotype matching can promote further divergence, and stronger choosiness can sometimes evolve to complete assortment (Matessi et al. 2001, Otto et al. 2008). Finally, when populations are spatially separated but exchanging migrants, choosiness can evolve to intermediate preference strengths similar to those that maximize divergent sexual selection (see Section 5; Servedio 2011, Yeh & Servedio 2015, Cotto & Servedio 2017). With separate preference and trait loci instead of phenotype matching, stronger choosiness may evolve during both sympatric speciation under disruptive selection (Doebeli 2005) (although this outcome is difficult to obtain; see Weissing et al. 2011) and reinforcement with secondary sympatry (Bank et al. 2012). In contrast, Servedio & Bürger (2014) found that when homogenizing preferences counter local adaptation of spatially separated populations, preferences will evolve to be weaker and weaker.

Sexual selection on choosiness can also be direct. This occurs when costs to choosiness reduce a female's own mating success. Theoretical models demonstrate that search costs will generally hinder speciation by directly selecting against stronger choosiness, potentially leading to the evolution of intermediate choosiness strengths or even random mating (e.g., Bolnick 2004, Bürger et al. 2006, de Cara et al. 2008, Doebeli 2005, Gourbiere 2004, Kirkpatrick & Nuismer 2004, Kopp & Hermisson 2008, Otto et al. 2008). Logically, this should be a general effect, regardless of whether preferences are separate from traits or result from phenotype matching. However, M'Gonigle et al. (2012) found that search costs combine with patchy population densities to result in frequency-dependent divergent selection on preferences, promoting population divergence (see also Bürger & Schneider 2006 for a case in which intermediate costs promote speciation).

The ideal empirical evidence to evaluate how the evolution of choosiness affects speciation would result from testing whether evolutionary change in choosiness is associated with changes in assortative mating among species and reductions in gene flow. These data are very difficult to obtain and are rare. Choosiness itself is hard to measure and has low heritability (Brooks & Endler 2001, Schielzeth et al. 2009). To reveal whether choosiness evolves and also influences speciation could be done by comparing choosiness in populations or species in early to late stages of speciation (possible in very few systems), for which population history is known, or between allopatric and sympatric populations. However, given the complexities identified by theory, even intermediately strong preferences can have substantial effects. One study shows that derived *Poecilia sulphuraria* females have weak mate preferences relative to ancestral *Poecilia mexicana* (Plath et al.

2010), indicating that choosiness has evolved to be weaker and reduces gene flow only from the derived to ancestral species. In a case of reverse speciation, historical data for threespine stickleback in a formerly reproductively isolated species pair show evolutionary weakening of mate preference and reduced sexual isolation resulting in substantial increases in gene flow (Lackey & Boughman 2013b). Rodríguez and colleagues (2013) report variable strength of preference for multiple populations within taxonomic groups, showing choosiness has evolved in those taxa.

Several studies reveal that the costs of choice modify choosiness by looking at plasticity in preference strength or choosiness in response to manipulating costs. For example, zebra finch females are less choosy when they are in low condition (Burley & Foster 2006). Few studies directly consider these effects on assortative mating or species recognition, however, although these implications have been considered for threespine stickleback (Kozak & Boughman 2015, Kozak et al. 2013, Tinghitella et al. 2015b). Although the effect of plasticity on the evolution of preference and speciation is well worth studying, it is beyond the scope of our review.

7. DISRUPTIVE SELECTION DUE TO MALE COMPETITION AND EFFECTS ON SPECIATION

Sexual selection includes both female mate choice and male competition. However, male competition has been largely ignored in speciation research. Given that competition over resources plays a central role in speciation via natural selection, this seems an obvious oversight. That competition among males over mating opportunities causes evolution of male mating traits is obvious by noting exaggerated weaponry and aggressive behavior of males (Emlen 2008). Female preferences and male competition may oppose each other or act in concert in their effects on assortative mating. Acting in concert strengthens overall sexual selection (Hunt et al. 2009) and can facilitate assortative mating even in the face of gene flow (van Doorn et al. 2004).

Several mechanisms of male competition have been theorized to facilitate speciation. Male competition that generates negative frequency-dependent sexual selection can foster divergence and speciation (Qvarnström et al. 2012, Seehausen & Schluter 2004) in a manner similar to the effect of ecological competition and natural selection (Dieckmann & Doebeli 1999, van Doorn et al. 2004). However, this may not always be seen (Tinghitella et al. 2015a) or may be insufficiently strong to cause speciation (Dijkstra et al. 2007), suggesting a need for additional theory and empirical tests. Instead, which male traits lead to successful reproduction may depend on the habitat in which competition and mating occur (Lackey & Boughman 2013a). Male competition between different species can generate a pattern of reproductive character displacement to avoid wasting effort on heterospecific competitors (Grether et al. 2009). In addition, there may be multiple ways to outcompete rival males, generating disruptive sexual selection for alternative phenotypes independent of their frequency (Keagy et al. 2016, McCullough et al. 2014). In the Keagy et al. (2016) study, differences between two species of stickleback fish in male competitive traits closely matched the fitness peaks that disruptive male competition generated, suggesting male competition played a large role in trait divergence and was also a source of sexual selection against hybrids. There are many fruitful research directions to pursue, including theoretical work to determine facilitating conditions and empirical work to test the effects that male competition has on isolation.

8. CONCLUSIONS: CAN SEXUAL SELECTION CAUSE SPECIATION ON ITS OWN?

Throughout this review, we have discussed theoretical and empirical work regarding whether sexual selection drives or hinders local adaptation and speciation (**Figure 2**). We conclude with the most stringent, and perhaps intriguing, form of this question: Can sexual selection *alone*, barring any role for natural selection, lead to speciation with gene flow? For sexual selection to be the sole cause, mating preferences themselves would have to diverge because of sexual selection. Although sexual selection can act directly on traits, it acts directly on preferences only if the preferences themselves lead to differential mating success of the females that carry them. For example, search costs are a form of direct sexual selection that can select directly on preferences. Selectively neutral preferences for arbitrary traits evolving under the Fisher process would not evolve owing to *direct* sexual selection, as preferences do not affect the mating success of females. They can be said, however, to evolve owing to *indirect* sexual selection, as sexual selection on the male trait leads to evolution of the female preference. Speciation can be facilitated by sexual selection in either case, although conditions are more stringent for indirectly selected preferences, which we elaborate on below. So what do models and empirical work tell us about the power of these forces?

The conditions for speciation by sexual selection alone have been the focus of several theoretical models. The quantitative genetic sexual selection model of Lande (1981), which ascribes speciation to sexual selection in the title, includes viability selection on the trait but shows that populations can drift to different points along a line of equilibria for trait and preference values even if there is a single trait optimum (see also Uyeda et al. 2009). This allopatric speciation by sexual selection cannot be maintained, however, if gene flow is introduced [this can be seen in Lande (1982) under the conditions of no underlying cline; also see Servedio & Bürger (2014)]. Sympatric speciation is the most challenging scenario. Although several models have found that sympatric speciation can occur by the joint action of two Fisherian processes in different directions (e.g., Arnegard & Kondrashov 2004, Higashi et al. 1999, Takimoto 2002, Takimoto et al. 2000, Turner & Burrows 1995, van Doorn & Weissing 2001), this process cannot occur without a mechanism that inflates preference variation (Weissing et al. 2011). In addition to the models described above, which have distinct preferences and traits, the phenotype matching models of Arnegard & Kondrashov (2004), which assumes sympatry, and Servedio (2011), which assumes spatial separation, both find that sexual selection alone can drive trait divergence, but this is limited (the latter additionally found that intermediate rather than strong levels of choosiness will evolve). We thus agree with the conclusion (Arnegard & Kondrashov 2004, Weissing et al. 2011) that although sexual selection alone has the potential to cause speciation, the conditions required are quite unusual.

Although ecological divergence is thus usually needed for speciation, in at least two situations sexual selection may be able to at least partially substitute for its effects. First, van Doorn et al. (2004) point out that male–male competition can substitute for disruptive viability selection and thus allow sympatric divergence by sexual selection alone. Second, sexual selection against hybrids can contribute to divergent selection, although it is unlikely to completely substitute for natural selection. Supporting empirical findings in numerous taxa show sexual selection against hybrids is a very strong isolating barrier relative to others (e.g., Lemmon & Lemmon 2010, Svedin et al. 2008). Sexual selection against hybrids can occur during the process of reinforcement, as is predicted by theory (Bank et al. 2012, Kirkpatrick & Servedio 1999) and shown empirically (e.g., Keagy et al. 2016, Lemmon & Lemmon 2010, Svedin et al. 2008). Sexual selection against hybrids can play a similar role during sympatric or parapatric speciation as populations bifurcate; bifurcation reduces the frequency of intermediate females, generating sexual selection against intermediate males (e.g., Otto et al. 2008).

These are fairly specific conditions, and empirical evidence demonstrating that sexual selection acts alone to cause speciation is lacking. Instead, empirical evidence suggests that natural and sexual selection almost certainly interact in their effects on speciation. Some of these studies leveraged the power of evolutionary replication (Schluter & Nagel 1995) by quantifying the effect of both sexual and natural selection and the resulting reproductive isolation for independently diverging, geographically variable populations. For example, divergence in multiple sexual and ecological traits is large and in parallel for multiple pairs of stickleback species, implying that sexual and natural selection work in concert (Boughman 2006, Boughman et al. 2005, Rundle & Boughman 2010), and this parallel divergence causes parallel sexual isolation (Rundle et al. 2000). In addition, meta-analyses of selection estimates in the wild suggest that the two forces often act to reinforce each other, typically both favoring more extreme trait values on one side of the distribution, at least for body size (Siepielski et al. 2009, 2011). However, natural and sexual selection can also act in opposition. In fact, the typical assumption is that sexual selection opposes natural selection—this is why sexually selected traits are costly (Andersson & Simmons 2006)—and examples have been found (e.g., Wikelski 2005). This highlights our earlier points that sexual selection may hinder divergent evolution and should not be expected to always enhance divergence.

The flip side of the question is whether natural selection often acts alone to cause sexual isolation. The byproduct mechanism (Dobzhansky 1951, Mayr 1942) posits that natural selection is the ultimate cause of speciation (Rundle et al. 2000, Schluter 2000) and that assortative mating occurs incidental to ecological divergence (McKinnon et al. 2004). Natural selection is unlikely to be the sole cause of sexual isolation, however, because divergent sexual selection can also contribute to assortative mating causing speciation (e.g., Boughman 2001, Grace & Shaw 2011, Kozak et al. 2011, Seehausen et al. 2008) and sexual selection is often as strong or stronger than natural selection (e.g., Siepielski et al. 2011). Even host-specialized insects provide relevant data, as their ecological divergence may initially be caused by natural selection (e.g., Wood & Keese 1990), but their mate choice is also affected by the host, generating divergent sexual selection and premating isolation (e.g., Rodríguez et al. 2006, 2008).

Moreover, several meta-analyses and reviews have argued that the joint action of natural and sexual selection is nearly always required for speciation (Kraaijeveld et al. 2011, Maan & Seehausen 2011, Marie Curie Speciat. Netw. 2011, Ritchie 2007, Safran et al. 2013). Given the many ways for natural and sexual selection to influence one another, it is not surprising that they often interact in the diversification process. The theoretical and empirical work we describe in this review demonstrates that, despite the many ways that sexual selection can contribute to speciation and local adaptation, its role is complex and its power as a possible driving force for reproductive isolation should not be overemphasized.

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