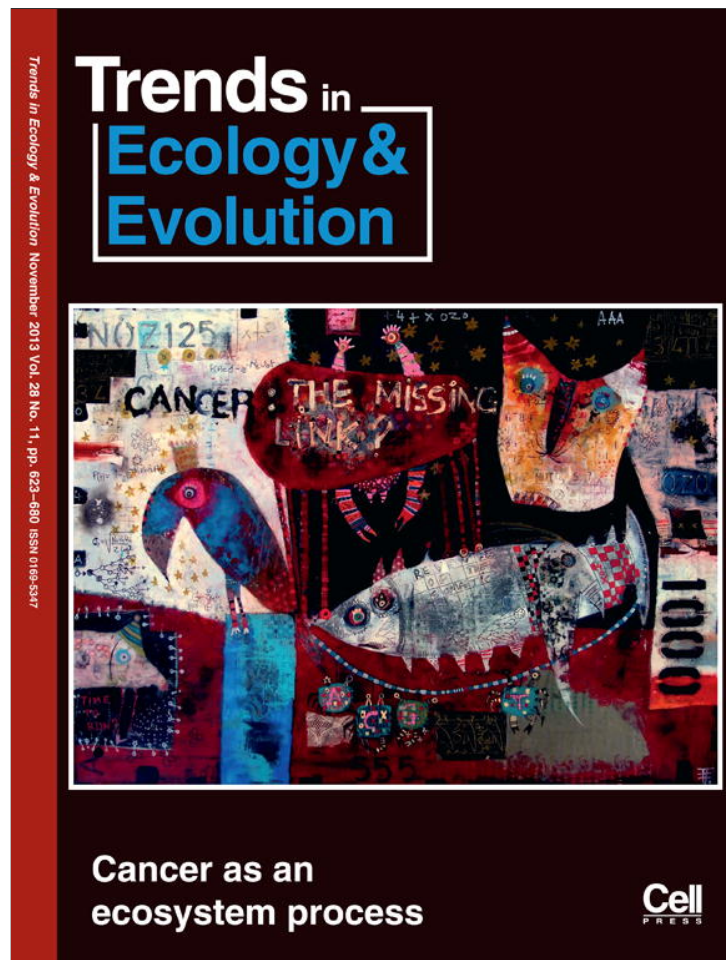


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# Contributions of natural and sexual selection to the evolution of premating reproductive isolation: a research agenda

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**Speciation by divergent natural selection is well supported. However, the role of sexual selection in speciation is less well understood due to disagreement about whether sexual selection is a mechanism of evolution separate from natural selection, as well as confusion about various models and tests of sexual selection. Here, we outline how sexual selection and natural selection are different mechanisms of evolutionary change, and suggest that this distinction is critical when analyzing the role of sexual selection in speciation. Furthermore, we clarify models of sexual selection with respect to their interaction with ecology and natural selection. In doing so, we outline a research agenda for testing hypotheses about the relative significance of divergent sexual and natural selection in the evolution of reproductive isolation.**

## Adaptive models of speciation

The origin of species remains an active area of research in evolutionary biology, and current interest centers on the interaction and relative importance of natural and sexual selection in speciation (see [Glossary](#)) [1–4]. Whereas compelling evidence exists for an important role of divergent natural selection in speciation (reviewed in [5–7]), consensus is lacking about the role of sexual selection in speciation. Speciation by sexual selection is thought to proceed most commonly via the divergent coevolution of male sexual signals and female preferences, leading to reproductive

isolation between populations [8–10]. Still, disagreement centers around whether sexual selection is a distinct process or a special case of natural selection [5,6,11], whether divergent sexual selection alone is an important driver of the evolution of reproductive isolation [9,10,12], or whether divergent sexual selection can result in speciation only in different ecological contexts (e.g., [1,3]).

A recent review [2] pointed out the various ways in which sexual and natural selection can interact during speciation via differences in the ecological context of divergence. Moreover, a second article [13] indicated that analyzing the interaction of natural and sexual selection is of primary interest for understanding the mechanisms underlying reproductive isolation, and that ‘future work needs to consider criteria for demonstrating a role for sexual selection compared with natural selection’ ([13], p. 31). Furthermore, two recent studies [14,15] called for greater precision in speciation terminology by outlining mechanisms related to ‘speciation by selection’ and ‘speciation without selection’ (i.e., polyploidy and drift), but differed on whether natural and sexual selection should be lumped [15] or distinguished [14] in a conceptual treatment of speciation by selection. In line with these calls for clarification, we pursue the following objectives: (i) to

## Glossary

**Behavioral pre-mating reproductive isolation:** absence or reduction of gene flow between groups due to phenotypic differences related to the process of mate selection or assortative mating.

**Ecological context:** the suite of biotic and abiotic conditions in which an organism lives.

**Fecundity:** number of gametes produced by an individual (usually eggs), also referred to as reproductive potential.

**Fertilization success:** proportion of gametes that form zygotes.

**Reproductive isolation:** absence or reduction of gene flow between groups due to genetic or phenotypic differences.

**Speciation:** divergence in phenotypes between two or more groups, ultimately leading to reproductive isolation.

**Trait:** measurable feature of a phenotype.

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elucidate natural and sexual selection as distinct processes of adaptive evolutionary change; (ii) to classify various models of sexual selection and their likely interaction with ecological context; and (iii) to outline an empirical framework for assessing the relative significance of natural and sexual selection in the evolution of reproductive isolation. Our overarching goal is to propose a synthetic research agenda on adaptive models of speciation with testable predictions about the relative contributions of both natural and sexual selection.

### Mechanisms of speciation by selection

#### *Sexual and natural selection as distinct mechanisms*

Disagreement surrounds a definition of sexual selection and whether it is a distinct mechanism of evolutionary change from natural selection [16]. Following Darwin [17], we define sexual selection as the result of the differential reproductive success that arises from competition for mates and access to fertilizations (see also discussions in [18]). We consider natural selection to be distinct from sexual selection: following a recent synthesis of speciation work [13], we adopt the definition of natural selection as the result of differential survival and fecundity of individuals in their current environmental context [13].

The distinction between natural and sexual selection is necessary for at least five reasons. First, sexual and natural selection operate in different ways: sexual selection favors trait variants that increase mate acquisition and fertilization, whereas natural selection favors trait variants that increase survival and fecundity. Second, when sexual and natural selection act on the same trait, they can act in opposition to one another (e.g., [19]): sexual selection can favor the exaggeration of a trait beyond, or in a different direction from, the naturally selected optimum. Accordingly, when one is interested in the mechanisms underlying trait distributions, it is important to consider the potentially opposing influences that natural and sexual selection can impose on phenotypic evolution. Third, there appear to be fundamental differences in the rate and strength of sexual and natural selection in nature, suggesting different evolutionary signatures of their effects. For example, evidence from a variety of studies and taxa indicate that the strength of sexual selection is greater than that of natural selection [20–22], and the direction of sexual selection appears more consistent over time compared with the direction of natural selection (e.g., [23]). Fourth, sexual selection is theorized to build linkage disequilibrium between preference–signal combinations more effectively than natural selection because nonrandom mating helps prevent the break up of linkage by recombination [24]; therefore, sexual selection might be particularly important in the process of speciation. Finally, one type of selection might contribute to divergence, whereas the second type inhibits it [25].

The above distinctions neither mean that speciation will often be driven by natural or sexual selection alone, nor that it would always be possible to demonstrate that a particular speciation event was the result of only one type of selection. For example, demonstrating that speciation was the result of sexual selection alone would require demonstrating that the environmental conditions experienced by diverging

populations were historically identical (or irrelevant to divergence) throughout the process of divergence. Conversely, one would have to demonstrate that mate preferences and all aspects of mating systems were identical throughout speciation to conclude that speciation was driven exclusively by natural selection. Instead, we emphasize the need to explore the relative contributions of natural and sexual selection to speciation, particularly those cases where divergence depends on their interaction. We suggest the best cases for these explorations are closely related and/or recently diverged populations. Although there is no guarantee that closely related lineages will ultimately attain reproductive isolation, we arguably cannot understand the origin of species without examining lineages in the earliest stages of divergence (i.e., at the origin). Study systems that enable examination of lineages with variable divergence times among closely related groups provide the best opportunities for investigating the roles of natural and sexual selection in the evolution of reproductive isolation. Accordingly, we focus here on the type of reproductive isolation that is most likely to be important during early divergence, and one that is most likely to interact with the environment: pre-mating isolation [10].

#### *Sexual selection can interact with ecology in diverse ways*

It is well established that the evolution of mating systems and mating strategies is affected by environmental factors, such as the spatial distribution of resources, population density, and operational sex ratio [26,27]. Indeed, behavioral ecologists have long studied the connections between ecological variation and the evolution of mating systems: mating systems tend to vary in the strength of sexual selection according to the ecological context in which selection is occurring (e.g., [26]). For example, social monogamy with biparental care is typically correlated with mate choice based on direct ecological benefits and weaker sexual selection compared with polygynous mating systems [4,26,28]. However, this relation between ecology and sexual selection has only recently gained traction in empirical and theoretical studies of speciation [1,2]. The exception is sensory drive studies [29], which deal with environmental influences on signal transmission and perception [30].

Ecological variables are known to influence mate choice in many different ways: communication systems are shaped by the sensory environment (e.g., [31]), expression of condition-dependent signals and preferences are limited by ecological factors such as food abundance and predation pressure (e.g., [32]), and mate choice is frequently based on environment-dependent aspects of the male phenotype, such as the quality of resources that a male can monopolize (e.g., [4,33]). Indeed, empirical data suggest that numerous environmental factors have broad and profound effects on variation in sexually selected traits and corresponding preferences both within and among populations [2,30,34,35], and these must be considered when determining the contributions of sexual and natural selection to speciation. These examples all suggest that natural and sexual selection work in synergy; considering either alone, one might draw the conclusion that selection is not strong enough to overcome the homogenizing force of gene flow, but together

**Table 1. Models of sexual selection and their likely interaction with environmental context<sup>a</sup>**

Type of model	Hypothesized interactions with the environment
<b>Direct benefits models</b>	
Males are chosen because they have traits or attributes that increase the fecundity or survival of their mates; common in socially monogamous species with biparental care	
Good parent model [37]	Interactions with environment are internal: preference for trait that indicates greater parental care, territory quality, mate provisioning, or territory defense
Efficient mate detection and localization [53,54]	Interactions with environment are external: preference for trait that is more effectively transmitted and received in a given environment (e.g., sensory drive: [29])
<b>Indirect benefits models</b>	
Mates are chosen because they have traits or attributes that indicate benefits for future generations via allelic inheritance; common in species with promiscuous mating systems and weak selection for biparental care	
Hamilton and Zuk [55], handicap model [56], and good genes [57,58]	Interactions with environment are internal: preference for trait that indicates heritable viability alleles, e.g., greater parasite and pathogen resistance (e.g., major histocompatibility haplotypes)
Darwin's model of sexual selection [17], Fisherian runaway [59], and sexy son [60]	Interaction with environment is minimal and/or unclear: preferences for trait are arbitrary but not associated with clear survival or fecundity benefits; male offspring inherit the phenotype of their father
<b>Conflict models</b>	
Conflict over mating drives antagonistic trait evolution	
Sexual conflict [40] and chase-away [61]	Interactions with environment are variable: reproductive outcomes determined by arms race conflict

<sup>a</sup>See Box 3 for definitions of environmental interactions.

they might increase the probability of speciation in the face of extensive gene flow.

To clarify the relative contributions of sexual and natural selection in speciation, we review the major classes of sexual selection model and point out the ways in which their different selective mechanisms are predicted to interact with ecological context and, thus, natural selection (Table 1).

### Clarifying different models of sexual selection

Most sexual selection models focus chiefly on female mate choice (as opposed to male choice or intrasexual competition) as a primary mechanism underlying 'benefits' models of sexual selection. Therefore, models of sexual selection are typically divided into three broad categories [36]: direct benefits, indirect benefits, and sexual conflict models (Table 1). In direct benefits models, females prefer traits that advertise how a potential mate can increase her fecundity or survival, such as through parental care or the defense of resource-rich territories (e.g., the good parent process [37] or the offer of nuptial gifts [38]). In indirect benefits models, females prefer male traits that advertise genetic benefits for their offspring, such as heritable components of attractiveness or immune system variation related to parasite resistance (reviewed in [39]). Finally, conflict models suggest that female preferences and male traits evolve via sexually antagonistic coevolution, and male traits do not necessarily advertise benefits for females, but are instead selected to manipulate their sexual response [40].

In both direct and indirect benefits models of sexual selection, interplay is predicted between ecological adaptation and mating success, although each model of sexual selection predicts different interactions with the environment (Table 1). The interaction between ecological adaptation and mating success is expected to be strongest in direct benefits models, where both traits and the preferences for them reflect benefits related to current environmental resources that are relevant for survival and reproduction. Indirect benefits models suggest interactions with the

environment as well, because signalers advertise alleles that confer high viability to shared offspring in the next generation. However, whereas signals with direct benefits advertise fitness benefits in the current environment (i.e., in 'real time'), indirect benefits lag by a generation. Temporal fluctuations in environmental conditions can alter the magnitude of indirect benefits and, thus, weaken the strength of selection. The environment can also affect sexually selected traits that evolve through conflict; for example, male guppies in high-predation populations engage in high levels of sneaky mating attempts and sexual harassment, thus compromising female choice [41]. Sexual conflict has also been shown to vary with population density [42] and population structure [43]. The only case in which ecology is predicted to have little effect on sexually selected traits is in cases of Fisherian runaway ('arbitrary') models, when benefits have no effect on, or correlation with, male or female survival or fecundity, unless signals become costly to maintain [39,44]. Yet, even in these cases, the environment can act as a transmission filter (e.g., song or color transmission might vary in different acoustic and light environments) and alter the dynamics of sexual selection (see 'external interactions' below).

### Testing the relative contributions of sexual and natural selection in speciation

Here, we highlight how reproductive isolation arises from divergent natural and sexual selection, clarify predictions that arise from different models of sexual selection, and consider how different models of sexual selection interact with ecology to generate reproductive isolation (Table 2, Box 1). The framework is designed to be applied to hybrid zones, sister species pairs, divergent populations, or any pair of lineages in which behavioral or ecological pre-mating reproductive isolation is still evolving. The application of this framework to populations in the early stages of divergence is most appropriate because if the groups being compared are old or reproductive isolation is long

**Table 2. Predictions of reproductive isolation for each mechanism of speciation and corresponding models of sexual selection<sup>a</sup>**

Hypothesis	Predominant adaptive mechanism underlying evolutionary change	Relevant measure of RI	Model of sexual selection	Predictions (empirical studies and common garden)	Signatures
Ecological adaptation alone	Divergent natural selection	Divergent ecological traits that yield a pattern of assortative mating independent of preferences for sexual signals (e.g., pattern of assortative mating by habitat or chronology)	N/A	No divergence in mate preference functions among ecotypes; pattern of mating is assortative by habitat or chronology; reproductive isolation breaks down in common garden	Ecology different, whereas sexual signals are not different
Sexual selection alone	Divergent sexual selection	Divergent sexual signals and concomitant divergent preferences for those signals	Darwin–Fisher models	Mate preferences are based on divergent sexual signals; behavioral reproductive isolation maintained in common garden	Ecology similar, whereas sexual signals are different
Sexual selection and ecological speciation (internal interactions with divergent environments)	Divergent natural and sexual selection	Divergent sexual signals that co-vary with ecological context and concomitant divergent preferences for those traits, where sexual signal divergence is tied to natural selection on signal expression	Internal: direct and indirect benefits models, conflict models	Divergence in sexual signals and corresponding preferences based on environmental sources of selection on traits; behavioral reproductive isolation can be maintained in common garden	Ecology different and sexual signals different
Sexual selection and ecological speciation (external interactions with divergent environments)	Divergent natural and sexual selection	Divergent sexual signals that co-vary with ecological context and divergent preferences for those traits, where sexual signal divergence is shaped by transmission efficacy in different ecological contexts	External: sensory drive	Divergence in sexual signals and their preferences is based on aspects of the environment that shape transmission efficacy; e.g., the light environment or signaling substrate; with altered environments, preferences might not be sufficiently diverged to generate reproductive isolation; behavioral reproductive isolation not necessarily maintained in common garden	Ecology different and sexual signals different

<sup>a</sup>Predicted patterns are those that indicate mechanisms of early population divergence when observed in closely related populations, subspecies, and ecotypes.

established, then the traits currently contributing to reproductive barriers might not be the ones that were important during divergence.

We also note that the use of proxies of sexual selection (e.g., dichromatism, extent of sexual dimorphism, mating system, or assortative mating) should be avoided, because they do not enable one to identify which model of sexual selection is at work in a particular study system (Box 2) [45].

*A trait-based approach*

We define signatures that indicate speciation by sexual selection, natural selection, and two types of interaction. The key to differentiating these signatures is to identify the type of trait or traits that cause pre-mating reproductive isolation (Box 1). These traits include features of behavior and morphology that are involved in mate selection, as well as corresponding preferences for those features. Because traits that affect mating and fertilization success evolve via sexual selection, finding reproductive isolation mediated by differences in such traits is a signature of speciation by sexual selection, and concomitant

divergence in both signals and preferences provides the strongest evidence of this process. Conversely, because traits that maximize survival or fecundity as a function of performance in specific habitats evolve by natural selection, finding reproductive isolation mediated by differences in such traits is a signature of speciation by natural selection. In a scenario involving natural selection alone, divergence in mate preferences is not required (Table 2).

The four conceptual models below should be viewed as locations on a continuum of adaptive models of speciation, with the ends representing greater contribution from either natural or sexual selection, and combinations of both mechanisms in the middle (Table 2).

*Reproductive isolation via natural selection*

Speciation by natural selection has been defined in various ways, most recently in [7] as a by-product of divergent natural selection, for example when selection related to obtaining resources in different populations works in contrasting directions. The most obvious signature of speciation by natural selection is ecological reproductive

**Box 1. Testing for the relative contributions of sexual and natural selection in speciation**

Here, we outline an approach to discern the relative significance of sexual and natural selection in speciation. A focus on traits used in mate selection or patterns of assortative mating will enable researchers to identify the relevant morphological and behavioral differences among closely related populations. The ideal case will include manipulative experiments such that causal associations between trait variation and patterns of survival, fecundity, and mate selection can be identified. The application of this framework is most suited to closely related populations, including subspecies and ecotypes.

**Step 1: determine which traits of all possible measurable trait differences are most divergent between closely related populations**

Empirical studies of phenotypic variation and divergence among closely related populations identify candidate traits that might contribute to reproductive isolation. A standardized effect size metric, such as delta P or Hedge's G [62], enables comparisons of divergence in different traits.

**Step 2: determine which of these divergent traits contributes to reproductive isolation**

Testing whether reproductive isolation is based on divergent preferences for divergent sexual signals, ecological differences, or both, is critical in assessing the relative contribution of natural and sexual selection to speciation. Identifying the traits used in pre-mating isolation can be done empirically through phenotype manipulations or studies of mate selection behavior.

**Step 3: empirically demonstrate the sources of selection shaping variation in the traits underlying reproductive isolation**

Trait variation related to survival (evasion of predators and parasites, or ability to procure important resources such as food

or shelter) is the raw material for natural selection; therefore, the relation between ecological trait variation and survival or fecundity should be documented. However, such a relation also opens the door to adaptive mate choice based upon these traits (including either or both direct and indirect benefits). Hence, studies that investigate only ecological traits might be correct in inferring a role for natural selection, but do not rule out a role for sexual selection. Patterns of mate selection based on divergent traits must be tested to illuminate whether sexual selection is at play. Experimentally manipulating trait values and measuring their effect on mating success is a straightforward means of testing sexual selection when possible.

**Step 4: determine the primary model of sexual selection at work within each population, if sexual selection is demonstrated**

Table 1 (main text) provides guidelines for determining whether direct, indirect, or conflict models of sexual selection better explain patterns of trait divergence among closely related populations. Each of these models makes different predictions about the interaction between sexual selection and ecological context.

**Step 5: measure variation in ecology**

Obvious ecological differences will be easy to define, but a lack of obvious ecological differences does not mean that ecological context is uniform. For obvious ecological differences, a classification of whether these are likely to interact with sexual signal production and expression ('internal') or whether they influence patterns of transmission and reception ('external') will help identify the potential interaction of sexual and natural selection in trait divergence [Table 2 (main text), Box 3].

isolation, due, for example, to divergence in habitat preferences [5,7] or timing of reproduction [46] that prevents individuals from different ecological contexts from coming into contact with each other. Thus, in cases of speciation due to divergent natural selection, patterns of assortative mating by ecotype arise as a function of individual habitat

choice and ecological adaptation to new environmental contexts, and not due to mate choice *per se*.

Many empirical and experimental studies support speciation by natural selection as being widespread and important in the evolution of new species (reviewed in [7]). We outline testable predictions for a predominant role of natural selection in speciation (Table 2), which is set up to contrast with other models of adaptive evolution that include a role of sexual selection.

**Box 2. The use of proxies for sexual selection**

Previous studies of the role of sexual selection in diversification have often used a comparative approach to test whether more 'sexually selected' clades are more diverse (reviewed in [12]). These studies typically use proxies of sexual selection, including mating system, sexual dimorphism and dichromatism, rather than actual measures of selection or reproductive isolation. A recent test of whether sexual dimorphism or dichromatism are good proxies for sexual selection was conducted within well-known study systems where the role of sexual selection in each population has been carefully studied [62]. This summary indicates that dichromatism and dimorphism are indeed robust estimates of sexual selection but that these are revealed after the fact, given that sexual selection has already been empirically tested in these systems. Accordingly, we prescribe caution in the use of proxies, such as dichromatism, dimorphism, and patterns of assortative mating, particularly in empirical studies where the direct action of sexual selection should be examined. Additionally, it is difficult to conduct standardized comparisons between dimorphic traits among populations when traits are measured in different units (e.g., brightness or frequency). This can be remedied by use of an unbiased effect size metric, which not only standardizes trait differences to comparable metrics, but also enables one to make direct comparisons between sexes and across study systems with signaling traits in different modalities [62]. It is not always reasonable to assume that vivid or conspicuous traits are under sexual selection. An empirical approach that includes characterizing the strength, direction, and causes of sexual and natural selection on phenotypic traits of interest is warranted whenever possible.

**Reproductive isolation via interactions of natural and sexual selection**

We distinguish two major ways in which ecology can interact with sexual selection: via internal and external interactions with sexually selected traits and preferences (Box 3). Distinguishing the type of environmental effects that shape variation in sexually selected traits and mating preferences is important, because internal and external interactions produce different predictions about the maintenance of reproductive isolation in common gardens and secondary contact (Table 2). Internal interactions occur when natural selection acts directly on the production and expression of sexual signals and mating preferences. In cases of internal interactions with the environment, sexual trait variation correlates with not only mating success, but also survival and fecundity. The basic case is one of pleiotropy, where the phenotypes under sexual and natural selection are one and the same; however, linkage disequilibrium between a naturally selected (viability) phenotype and a sexually selected phenotype also would facilitate their coevolution and represents another type of internal interaction between the environment and sexual selection (Box 3). In either case, variation in sexual signals and mating preferences is

**Box 3. Internal versus external interactions with the environment**

We distinguish two ways in which the environment can affect divergence in sexually selected traits and the preferences for them: internal and external interactions. Each makes specific predictions about the sources of selection on sexual traits and results in different signatures in empirical studies (see [Tables 1 and 2](#), main text).

Internal environmental interactions occur when natural selection acts on the production and expression of sexual signals and preferences either directly, through pleiotropy, or indirectly via linkage disequilibrium. In this case, traits that affect mating success (or traits linked to those that affect mating success) are associated with variation in survival or fecundity. Such traits are sometimes called 'magic traits' [63,64] and often will occur when features of the environment influence strategies of resource allocation to signal traits. An example includes nonrandom mating based on bill morphology in swamp sparrows [65]. Reinforcement of species-specific signals and preferences due to the reduced fitness of hybrids [66] is also an example of an internal interaction, typically because of linkage disequilibrium between viability alleles in hybrids that experience negative natural selection and the signal and preference alleles that led to the generation of those hybrids [67]. Because of their direct interaction with ecological context, sexual signals that are influenced by natural selection tend to be those that advertise condition or the ability to withstand the costs of signal expression as predicted by direct and indirect models of sexual selection ([Table 1](#), main text).

External environmental interactions are cases in which signals and preferences vary as a function of transmission efficacy and reception in different habitats. Here, variation in signals or preferences affects mating success but is not correlated with survival or fecundity.

Models of sensory drive ([Table 1](#), main text) are a clear example of external interactions, where aspects of the environment act as filters affecting signal detectability and perceptibility, and sexual selection favors more detectable or perceptible trait variants [29,30]. Character displacement due to heterospecific competition (e.g., signal jamming) is another potential external interaction [68].

Internal and external interactions need not be mutually exclusive. A given signal or preference could be affected by the environment in both ways, and certain environmental factors might have both external and internal interactions with trait expression. For example, population density might interact externally with sexual selection if a high density of conspecifics creates a noisy environment that affects mating success and favors a change in signaling strategies [69]. It might also interact internally, if higher population density results in stronger competition for mates and ultimately greater survival costs of investment in sexual signaling [34]. In these cases, clarifying the social function of sexual signals (e.g., in terms of their use in dominance hierarchies) can help predict patterns of divergence in different environments.

In [Table 1](#), we classify effects of ecological factors on variation in sexually selected phenotypes as 'internal,' 'external,' or 'internal + external'. In doing so, we leverage the descriptions of ecological variables outlined in [2] and include explicit predictions for their potential role in divergent sexual selection. Although the effects of these environmental variables on sexual selection and mate choice have often been studied within populations, our predictions are concerned with how environment and sexual selection vary and covary between populations, which has been the topic of considerably less empirical study and is a critical area for further research.

**Table 1. Examples of ecological factors that can contribute to variation in expression and development of sexually selected traits<sup>a</sup>**

	Interaction between sexual signal and preference evolution and ecological context	Examples
<b>Internal effects</b>		
Dietary resources	Variation in carotenoid-based color influenced by carotenoid availability in the environment	Orange spots in guppies [70]
Predators	Relative elaboration of ornaments constrained by predator presence	Calling behavior in crickets [71]
Parasites	Relative elaboration of traits constrained by variation in parasite prevalence and virulence	Parasites in sticklebacks [72]
Heterospecifics	Presence of incompatible heterospecifics leads to indirect selection against hybridization through linkage disequilibrium with hybrid inviability (reinforcement)	Body size in spadefoot toads [73]
Climate	Differences in climate constrain expression of costly traits	Temperature and lion manes [74]
<b>External effects</b>		
Abiotic sensory environment	Signals evolve for optimal transmission, leading to divergence in different environments	Nuptial color in sticklebacks [31]
Biotic sensory environment	Variation in heterospecific assemblage leads to shifts in signal space used	Acoustic signaling in frogs [75]
<b>Internal + external effects</b>		
Population density	External effects through signal disruption; internal effects through variation in resource allocation among life-history stages and mating strategies	Song length in willow warblers [76]; aggressive behavior in guppies [77]

<sup>a</sup>We divide these interactions into internal, external, and internal + external categories, reflecting the different sources of selection that underlie trait variation.

explained by environment-related differences among individuals, either in signal or perception (hence 'internal'). In cases of external interactions, sexual trait variation correlates only with mating success, and a particular ecological context influences the efficiency of transmission and reception between senders and receivers ([Box 3](#)). Here, divergence in signals or signal perception is caused by differences among environments (hence 'external').

*Sexual selection affected by ecological context through internal interactions.* In these scenarios, sexual signals and their corresponding preferences affect survival and fecundity directly, or they are closely linked to viability traits, and are thereby influenced by both sexual and natural selection ([Table 2](#)). Most direct and indirect models of sexual selection include a role of ecological context in shaping trait variation in closely related populations,

because preferences for these traits are only advantageous in a specific environment. Internal interactions include traits that are highly condition dependent, such that their development and expression advertise something about the ability of an individual to procure resources in a particular ecological context (*sensu* [1]). For example, differences in parasite infections among closely related populations might be an aspect of ecological context that is advertised through variation in sexual signals (reviewed in [47]). Moreover, mate choice for condition-dependent traits might promote local adaptation and, thus, divergent trait–preference associations as populations become isolated in different environments [48,49].

**Sexual selection affected by ecological context through external interactions.** In this case, features of the signaling environment influence sexually selected signal transmission and reception and, thus, signal evolution. External environmental effects are most likely to be abiotic ecological factors, such as light or acoustic environments or signal medium (e.g., turbid versus clear water). However, population density or sympatric species with overlapping signal values can also influence the transmission of a signal, and might result in signal divergence if the amount of interference differs across environments. In the external case, trait variation affects only mating or fertilization success, and trait divergence occurs primarily due to variation in signaling environment rather than in how the environment shapes the information content of the signal itself (Table 2, Box 3).

**Reproductive isolation via sexual selection alone** Previous definitions of speciation by sexual selection (e.g., [8,18]) require divergent signal and preference coevolution in closely related populations, such that sexual selection *per se* can be identified as the cause of reproductive isolation, rather than the buildup of genetic differentiation due to geographic isolation or ecological adaptation.

Quantitative models indicate that speciation by sexual selection alone is possible typically as divergent Fisherian runaway selection [50]. Given that all other sexual selection models indicate an interaction with ecological context (Table 1), cases where sexual selection alone has a predominant role in speciation might be rare (but see e.g., [51,52]). It is unclear whether empirical examples of sexual selection with a primary role in speciation have also simultaneously and systematically investigated a role for ecological context. This is an important avenue of future research.

### Concluding remarks and future directions

Here, we have distinguished sexual selection as a mechanism of adaptive evolution distinct from natural selection and have clarified differences among models of sexual selection. Different models of sexual selection vary in their predicted interactions with ecological context during the evolution of reproductive isolation. Direct benefits models include an important role of current ecological context in divergent sexual selection between closely related populations, and variation in traits and mating preferences should be tightly tied to variation in the current environment. Indirect benefits selection relies on honest signaling

of ‘good genes’, typically related to parasite resistance or other features of individual condition, but does not operate in a ‘real time’ ecological context as do direct benefits. Fisherian sexual selection appears to be the only model that does not require a major role of the ecological context.

Our proposed framework offers guidelines for empirically determining the relative significance of natural and sexual selection in speciation (Box 1). We suggest a trait-based approach that identifies phenotypic features that cause reproductive isolation among closely related populations and is one that is amenable to experimental study. Determining the importance of natural and sexual selection in shaping the traits that cause reproductive isolation, and sorting out which model of sexual selection shapes signaling traits, will be critical for determining how ecological context is likely to interact with sexual signal divergence (Box 1). Conducting these studies in natural settings will better illuminate the features of ecology that differ in meaningful ways between divergent populations. Finally, the use of proxies for sexual and natural selection have their place in large-scale phylogenetic studies, but actual measures of sexual and natural selection should be used in empirical investigations. By gathering the data necessary to distinguish the relative significance of each adaptive model of evolution in speciation, we can better piece together the variety of mechanisms that generate biological diversity.

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