Review

Speciation by sexual selection: 20 years of progress

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Twenty years ago, a seminal paper summarized the role of sexual selection in speciation as the coordinated evolution of (male) courtship signals and (female) preferences leading to prezygotic (behavioral) isolation between divergent lineages. Here, we discuss areas of progress that inspire an updated perspective. First, research has identified multiple mechanisms of sexual selection, in addition to female mate choice, that drive the origin and maintenance of species. Second, reviews and empirical data now conclude that sexual selection alone will rarely lead to reproductive isolation without ecological divergence, and we discuss the assumptions and possible exceptions underlying that conclusion. Finally, we consider the variable ways in which sexual selection contributes to divergence according to the spatial, temporal, social, ecological, and genomic context of speciation.

The role of sexual selection in speciation

The power of selection to drive **speciation** (see Glossary) is a continued focus of evolutionary research [1–5]. Selection causes changes in traits and associated genes that affect the relative fitness of individuals; when those changes cause divergence among populations, selection can drive speciation. Traits can affect relative fitness in multiple ways, and these can be roughly categorized into traits that affect survival and fecundity, which evolve due to **natural selection**, and traits that affect mating and fertilization success, which evolve by **sexual selection** [6–9]. Most of Darwin's first book [6] and many monographs thereafter [1,10] focus on traits that affect survival or fecundity, generating a framework of speciation by natural selection as organisms adapt to different environments. However, sexual selection also can have an important role in speciation.

The modern working definition of speciation by sexual selection, adopted and adapted in multiple literature reviews [2,3,8,11–13], was provided by Panhuis *et al.* [2] in a special issue of this journal in 2001. They wrote: 'Speciation, the splitting of one species into two or more, occurs by sexual selection when a parallel change in mate preference and secondary sexual traits within a population leads to prezygotic isolation between populations, and when this is the primary cause of reproductive isolation.'

The paper by Panhuis *et al.* [2] was partly a summary of the research inspired by West Eberhard [14] and Lande [15], whose work formed the foundation of the field during the last part of the 20th century. It was also a critical response to studies that tested whether sexual selection accelerates speciation using comparative analyses [16–18] (for meta-analysis, see [12]). Panhuis *et al.* [2] emphasized that, if speciation is defined as the evolution of **reproductive isolation**, then these types of comparative study cannot convincingly demonstrate speciation by sexual selection because they do not demonstrate **behavioral isolation**. Their paper was a clarion call for the field. It provided a clearly defined research agenda to guide empirical tests of this central hypothesis, and it remains an important guiding framework of research today [19].

Highlights

We revisit a seminal paper on sexual selection and speciation published two decades ago by Panhuis *et al.* in *TREE*.

Our understanding of the role of sexual selection in speciation has expanded over the past 20 years.

Several different mechanisms of sexual selection beyond female choice contribute to speciation.

Sexual selection and its interactions with ecological, temporal, spatial, social, and genomic context have important and varying roles in speciation.

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Expanding upon several reviews of the field [3,8,11,13], we summarize three areas of progress to account for: (i) the contribution of sexual selection mechanisms other than female mate choice; (ii) the role of ecological adaptation throughout speciation; and (iii) the role of sexual selection in different spatial, temporal, social, ecological, and genomic contexts of speciation. The purpose of this review is to celebrate the seminal contribution of Panhuis et al. [2] with updates on our understanding of the role of sexual selection in speciation that reflect progress in this rich field over the past 20 years (Table 1).

The myriad mechanisms of sexual selection

Panhuis et al. [2] position **premating** mate choice, especially female preferences of male traits ([2] p. 370), as the primary mechanism of speciation by sexual selection. Indeed, the primary literature and reviews [3,8,11,13] on speciation by sexual selection mostly focus on the coevolution of female mate choice and male ornaments. Through this lens, the receiver psychology of females and the benefits of their choices are paramount, and behavioral isolation is the defining endpoint. However, research has expanded over the past 20 years to explore mechanisms other than female mate choice in speciation (Table 2).

For example, male mate choice has received increasing empirical and theoretical attention since 2001 [20,21]. Females of many species exhibit secondary sexual traits that differ between populations and, in many cases, males prefer aspects of female ornaments within populations [22–24], suggesting that male choice contributes to both behavioral isolation between species and sexual selection within species. Male choice may have been overlooked in favor of female choice because most work on speciation by sexual selection focuses on sexually dimorphic lineages with elaborate males and presumably choosy females [12]. However, work in *Drosophila* and Lepidoptera clearly demonstrates the importance of male mate choice in reproductive isolation [25,26]. Future research investigating the intersection of sexual dimorphism, male mate choice, and speciation could help resolve this apparent discrepancy.

Cryptic female choice also can contribute to speciation [27]. When females mate with multiple males, any mechanism that biases paternity toward one of those mates is a form of cryptic female choice. Cryptic female choice can occur in **perimating** or **postmating** interactions, when some characteristic of female physiology or behavior biases paternity toward sperm of one male, presumably with a fitness advantage for the female or her offspring. Many examples of speciation by cryptic female choice are of conspecific sperm outcompeting heterospecific sperm in sympatric free-spawning marine invertebrates, although similar results have been observed in birds and insects (Table 2). Additional work on processes such as sperm competition and sexual conflict, which can drive divergence in gamete recognition and reproductive tract proteins, is key to identifying the role of cryptic mate choice in speciation.

The role of premating intrasexual contests in speciation gained attention when Seehausen and Schluter [28] observed that African cichlid fish color morphs in close physical proximity were more likely to be of a different, rather than similar, color. They proposed a mechanism of speciation via male–male competition whereby rare competitive phenotypes enjoy a negative frequency-dependent advantage when males bias aggression toward similar, common phenotypes. Their model applies primarily to sympatric speciation; however, male–male competition also clearly drives phenotypic divergence among allopatric populations, evidenced by widespread diversity in sexual weapons among geographically isolated species and populations [29]. Whether premating intrasexual contests can lead to reproductive isolation is a matter of debate [30–32], but agonistic character displacement can promote reproductive isolation between divergent lineages upon secondary contact [33], implicating a role of male–male competition in at

Glossary

Behavioral isolation: a type of premating isolation in which gene flow between evolutionary lineages is restricted due to heritable differences in mating communication signals and preferences.
Geographic isolation: a reduction or absence of gene flow between evolutionary lineages due to a geographic barrier to dispersal rather than to heritable trait differences.
Natural selection: selection that arises from fitness differences associated with competition for survival or fecundity; also called ecological selection or viability selection.
Perimating: time during the act of mating or fertilization during which physical interactions between mates occur.
Postmating: time after mating or fertilization is complete during which interactions can occur between (e.g., gametes, the female reproductive tract and seminal fluids, pair-bonded mates, and/or parents and offspring).
Preference function: relationship between variation in signal value and the response to that signal value in a receiver.
Premating: time before mating or fertilization during which interactions between potential mates occur.
Reproductive isolation: reduction or absence of gene flow between evolutionary lineages due to differences in one or more heritable traits that act as reproductive barriers.
Sexual selection: selection that arises from fitness differences associated with competition for access to gametes for fertilization.
Sister populations: groups of individuals that are most closely related phylogenetically; they share a most recent common ancestor but have diverged to some extent due to restricted gene flow.
Speciation: the splitting of one species into two or more.

Table 1. Signatures of the contribution of sexual selection to speciation, then and now

Original signature [2]	Progress	Revised signature	Empirical test
Substantial differences occur among populations or species in male sexually selected traits with correlated female preferences	Multiple mechanisms of sexual selection can drive speciation	Substantial differences occur among populations or species in sexually selected traits	Between-population analyses of phenotype variation (e.g., delta P or Hedges G) [94] *or*
			For closely related populations, within-population analyses in natural environments (if possible) to test whether phenotype variation is correlated with variation in mating and fertilization success [95]
Changes are sufficient to result in prezygotic isolation should populations come into contact	Speciation may not involve secondary contact, either because allopatric species may never come in contact, or because speciation was sympatric *and*	Evolutionary lineages are described as taxonomically distinct species on the basis of differences in sexually selected traits *or*	Determine whether species-diagnostic phenotypes affect mating or fertilization success *or*
	Multiple mechanisms of sexual selection can lead to different types of reproductive isolation	Changes in sexually selected traits are sufficient to result in reproductive isolation	Manipulate candidate phenotypes or genotypes to test their effect on reproductive isolation [96]
There is little genetic differentiation between populations or species, suggesting rapid divergence	Genetic divergence is heterogeneous; there may be regions of the genome with high levels of divergence *and*	Regions of the genome associated with sexually selected traits show increased divergence relative to other regions	Whole-genome analysis to analyze population-level differences in genomic architecture associated with genotype–phenotype mapping [97]
	Speciation caused by sexual selection is not necessarily rapid		
There is little or no reduction in hybrid viability or fertility, although hybrid fitness might be reduced by inappropriate signals or preferences	Different mechanisms of sexual selection can lead to postmating isolation, including hybrid inviability and sterility	None	
If applicable, there is no character displacement	Character displacement can result from both natural and sexual selection and may be necessary to complete the speciation process	If present, character displacement is driven by sexual selection, and sympatric populations experience little to no gene flow because of displaced sexually selected traits	Determine whether displaced signals or preferences are heritable and vary with mating or fertilization success *or*
			Manipulate displaced signals or preferences to test their effect on reproductive isolation

least one spatiotemporal context of speciation (see later). Mendelson *et al.* [34] also propose a role for male–male competition in the evolution of reproductive isolation among allopatric populations, hypothesizing a pleiotropic basis of male and female choice.

The role of postmating intrasexual contests in speciation is largely framed as sperm competition leading to fertilization barriers [35,36]. Species in numerous taxa exhibit rapid divergence in sperm-related DNA and many show patterns of positive divergent selection [37–40]. Changes in sperm alone are not likely to be sufficient for reproductive isolation, which requires concomitant changes in egg surface proteins or features of the reproductive tract [35]. One way such coevolution might occur is if egg proteins evolve neutrally, in which case sperm will evolve to maintain compatibility [36,37,39,41]. Sperm–egg coevolution also can occur at low population densities, when selection favors changes that increase the compatibility of sperm and egg recognition proteins [37,42,43]. More commonly, however, sperm competition is thought to generate reproductive isolation through sexual conflict, such as the antagonistic coevolution of sperm and egg surface proteins [35–37].

Sexual conflict is a difference in the 'evolutionary interests' of males and females that can result in sexually antagonistic selection [44–46] and speciation [47–50]. In general, males benefit more

Table 2. Empirical examples of speciation by mechanisms of sexual selection other than female mate choice

Mechanism	Taxon	Evidence provided[a]	Refs
Male mate choice	Sagebrush lizards, *Sceloporous graciosus*	Males prefer females of own population	[98]
	Darter fish, *Etheostoma* spp.	Males prefer females of own species	[34,99]
	Cichlid fish, *Labeotropheus fuelleborni*	Males prefer females of own population	[100]
	Wall lizards, *Podarcis muralis*	Males prefer females of own population in a contact zone	[101]
	Leaf beetles, *Chrysochus cobaltinus* and *Chrysochus auratus*	Males prefer females of own species in a contact zone	[102]
	Field crickets, *Gryllus firmus* and *Gryllus pennsylvanicus*	Males prefer females of own species	[103]
	Demoiselle damselflies, *Calopteryx splendens* and *Calopteryx virgo*	Males prefer females of own species	[104]
	Heliconian butterflies, *Heliconius melphomene* and *Heliconius cydno*	Males prefer females of own species	[26]
	Fruit flies (e.g., *Drosophila simulans*)	Males prefer females of own species	[105]
Cryptic female choice	Flycatchers, *Ficedula albicollis* and *Ficedula hypoleuca*	Females inhibit heterospecific sperm performance	[106]
Male-male premating competition	Darter fish, *Etheostoma* spp.	Bias aggression toward males in species of similar color (allopatric)	[99]
	Dung beetles[b], *Onthophagus* spp.	Dramatic diversity in male weapons	[29]
	Ungulates[b], various species	Dramatic diversity in male weapons	[107]
	Darter fish, *Etheostoma caeruleum* and *Etheostoma spectabile*	Sympatric males bias aggression toward conspecific males more than allopatric males do	[108]
	Wall lizard, *Podarcis muralis*	Males of one population outcompete the other for preferred females in a contact zone	[101]
	Cichlid fish, *Metriaclima mbenjii*	Bias aggression toward males in species of similar color (sympatric)	[109]
Male-male postmating (sperm) competition	Multiple taxa[c]	Rapid evolution of sperm-related fertilization genes	[38]
	Fruit flies[b], *Drosophila* spp.	Accelerated evolution and positive selection of testis-specific genes, male seminal fluid proteins, and spermatogenesis genes	[110]
Premating sexual conflict	Seed beetles[b], Bruchidae	Coevolution of male genital spines and female reproductive tract	[111]
	Water striders[b], *Gerris* spp.	Coevolution of male and female reproductive structures	[112]
	Harvestmen[b], Leiobuninae	Coevolution of male and female reproductive structures	[113]
	Dung flies, *Sepsis cynipsea*	Preference for own line in experimentally evolved high conflict lines	[114]
	Fruit flies, *Drosophila melanogaster*	Prezygotic isolation due between experimentally evolved lines due to reduced female resistance	[115]
Postmating sexual conflict	Arthropods[b], multiple species	Higher speciation rates in polyandrous species	[116]
	Abalone, *Haliotis* spp.	Rapid evolution of lysin (sperm protein) and VERL (egg protein)	[39]
	Sea urchins, *Strongylocentrotus* spp. and *Echinometra* spp.	Rapid evolution and positive selection of su-bindin (sperm-binding protein); highest rates in sympatric species; assortative fertilization	[37,41]
	Fruit flies, *Drosophila* spp.	Positive selection of male ejaculate proteins and female receptors	[39]
	Mammals[b], multiple species	Positive selection of several female reproductive proteins	[117]

[a]Refers to evidence put forward as consistent with a role of sexual selection in speciation, if not necessarily demonstrative [11].
[b]Broad comparative studies.
[c]Rapid evolution of fertilization proteins is consistent with both sperm competition and postmating sexual conflict.

than females from increased mating success [6,51], generating a conflict between the sexes about the ideal number of matings. Conflict can occur in premating, perimating, or postmating interactions [52], and conflict can entail natural as well as sexual selection. If female survival or fecundity is reduced due to a male-benefitting phenotype, then female resistance will evolve

due to natural selection, while male phenotypes evolve due to sexual selection. Antagonistic interactions between male ('persistence') and female ('resistance') phenotypes within species can lead to morphological elaboration, coevolution between male and female alleles, and reproductive isolation [47–49]. Indeed, Rice [49] argues that sexual conflict may be the dominant force generating reproductive isolation among sexually reproducing populations. Sexually antagonistic coevolution of gamete recognition proteins can lead to divergence independent of ecological differences [53], a case that merits further attention when asking whether sexual selection alone can drive speciation (see later).

In summary, myriad mechanisms of sexual selection can lead to population divergence, resulting in not only a breathtaking diversity of conspicuous and often bizarre sexual ornaments, but also of phenotypes less obvious to humans. This divergence might also generate reproductive isolation between lineages, not simply premating behavioral isolation, but multiple forms of premating, perimating, and postmating reproductive isolation that restrict interbreeding [54]. To researchers immersed in the field, the contribution of mechanisms other than female mate choice may appear obvious, but this pluralistic perspective is not yet fully integrated into syntheses of speciation by sexual selection [2,3,8,11,13].

The role of natural (viability) selection

A second area of progress concerns the interaction of natural selection, ecological adaptation, and sexual selection in speciation. The consensus of recent reviews is that speciation is most likely to be driven by a combination of these mechanisms, rather than by sexual selection alone [3,8,11,13] Maan and Seehausen [13] and Safran *et al.* [11] clarified at least two ways in which habitat differences can lead to local adaptation of mating traits and, thus, alter the direction of sexual signal or preference evolution. One way is when distinct habitats exert divergent selection pressures on sensory systems, thus generating novel preferences that, in turn, lead to divergent selection on signals. The African cichlid species pair *Pundamilia pundamilia* and *Pundamilia nyererei* is a well-developed example. *P. pundamilia* lives in shallow water with full-spectrum light; females are more attracted to the color blue over red, and males have blue nuptial color. Its sister species, *P. nyererei*, lives in deeper water with red-shifted light; females prefer red over blue, and males have red nuptial color [55]. Cases such as this, with divergent selection on preferences, are more likely to lead to behavioral isolation than are cases of the second type (see next paragraph), because preferences and signals must both diverge for behavioral barriers to be maintained in the shared environment of secondary contact [56].

A second way that habitat differences can alter the trajectory of sexual selection is by affecting the transmission of signals, which then diverge to maximize transmission under local conditions [57,58]. Here, divergence by local adaptation can lead to distinct mating signals but may not necessarily lead to reproductive isolation. For example, male lizards in the genus *Anolis* display a colorful dewlap that differs among species in spectral quality and brightness. For some species, the dewlaps are highly contrasted (detectable) against the background of their own habitat, whereas they are less detectable against the background of the habitats of other species [59]. In this case, a universal preference for high contrast might select for different dewlap features in different habitats, but that same preference should promote signal convergence in secondary contact if lineages come to occupy the same light environment, which in turn may lead to hybridization. Indeed, signal convergence resulting from the interaction of natural and sexual selection in similar environments, and the potential impact of that convergence on the fate of divergent lineages, is an understudied outcome of secondary contact [60,61]. Of course, whether divergence of this second type can drive speciation *per se* depends on whether reproductive isolation is a defining criterion (see later).

One of the signatures proposed by Panhuis et al. [2] is rapid sexual trait evolution (Table 1), namely that speciation by sexual selection should leave a signature of rapid evolutionary change in sexual traits but not viability traits. On average, sexually selected traits experience stronger selection [62] over longer timescales [63] than do viability traits, and they may be the first traits to evolve among diverging populations. However, theoretical work over the past 20 years suggests that divergent sexual selection alone is not likely to result in reproductively isolated lineages. For allopatric speciation, the Fisher–Lande–Kirkpatrick model of indirect selection on female preferences [15], the most highly cited model of speciation by sexual selection [19], appears insufficient to generate reproductive barriers upon secondary contact [64,65]. For sympatric speciation, disruptive sexual selection is unlikely to result in reproductive isolation without accompanying disruptive natural selection on mating traits [66] (but see [67]). Indeed, 'magic traits' (traits involved in mate choice that also evolve due to local adaptation) may not be as rare as previously thought [68]. These analyses contribute to the current conclusion that sexual selection alone rarely drives speciation, and suggest that rapid and exclusive divergence in sexually selected traits is not a reliable signature of speciation by sexual selection. However, that conclusion is rooted in reproductive isolation as a defining criterion of species and models of indirect selection on behavioral preferences. Arguably a more inclusive interpretation of speciation (see later) or sexual selection (e.g., antagonistic coevolution of sperm and egg recognition traits independent of ecology) deserves consideration before ruling out one of the central themes of Panhuis et al. [2] (see also [5]): rapid speciation by sexual selection alone (see Outstanding questions).

Therefore, a central goal for the next 20 years is to determine how different sources of selection act alone or in concert to drive trait diversification and the evolution of reproductive isolation. Safran et al. [11] (see Box 1 therein) laid out a series of five steps to empirically test the contributions of natural and sexual selection to speciation. The steps are ambitious and best applied to closely related populations in early stages of divergence. The last of these steps (quantifying variation in ecological context to assess the opportunity for divergent natural selection) is the most challenging, because subtle differences can remain undetected but are critical to the organisms under study (see [69]). However, the remaining steps outline a tractable research agenda to identify the trait differences that diagnose species and determine the sources of selection driving their divergence.

Sexual selection and the contexts of speciation

Finally, research over the past 20 years has embraced speciation as a highly variable process [70–75]. For example, speciation can be characterized by different spatial, temporal, social, ecological, and genomic contexts from one diverging lineage to another. Conceptualizing speciation as a continuum along each of these contexts clarifies the role of sexual selection, especially when it might be sufficient to drive divergence on its own, when it is likely to interact with divergent ecological selection, and when it is not likely to contribute at all. Species complexes or species-rich genera that contain populations and species in a range of these contexts are particularly instructive for investigating when and how sexual selection may (or may not) lead to speciation [56].

Spatial and temporal context

The spatial context of speciation refers to the geographical relationship of diverging lineages, roughly categorized as allopatric, parapatric, or sympatric [54,76]. Temporal context refers to the chronology of divergence, ranging from early (when populations begin to diverge genetically and phenotypically) to late [when divergent populations may (or may not) be reproductively isolated]. In some cases, for example, **sister populations** are **geographically isolated** during the early stages of speciation (i.e., 'allopatric speciation'). They may then expand their ranges into parapatry (secondary contact), and ultimately may transition into sympatry during the late stages of the

process. In other cases, the spatiotemporal context is reversed (i.e., 'sympatric speciation'). Populations in these cases overlap in space during the early stages of divergence and only later may experience range expansion into parapatry or allopatry. The spatial and temporal contexts matter not only because they affect the likelihood of gene flow and recombination, but also because they affect the social and ecological contexts of speciation, both of which impact the way in which sexual selection contributes to divergence [73,77,78].

Social context

Social context here refers to the presence/absence of a sister population. In early allopatric speciation, sister populations do not overlap in space and, therefore, do not influence the dynamics of sexual selection. Given that individuals run less risk of mating with an incompatible partner in allopatric populations, we might expect relaxed selection on **preference functions** that, in turn, can facilitate the evolution of novel signals [79]. Sexual selection alone can have a large impact on divergence in these cases [2,15]. In secondary contact, by contrast, sister populations co-occur and are potentially divergent, such that the risk of mating with an incompatible individual can strongly influence the evolution of mate choice, for example via reinforcement [80,81]. During reinforcement, natural selection against hybrids indirectly favors the divergence and/or narrowing of preference functions, which can lead to variation in mating and fertilization success and complete reproductive isolation [82]. During early sympatric speciation, as in secondary contact, the presence of a sister population is a defining feature, but here the cost of mating across sister populations is initially extremely low. In this case, disruptive natural selection is thought to be necessary to overcome the homogenizing effect of gene flow due to permissive mate choice; sympatric speciation is a case where sexual selection alone is thought to be insufficient to drive divergence [66].

Ecological context

Ecological context refers to the abiotic and biotic features of habitats occupied by diverging lineages. Ecological differences are challenging to measure, but different spatiotemporal contexts can be reasonably associated with different ecological contexts, which in turn affect the role of sexual selection in speciation. During early allopatric speciation, diverging populations are likely to experience different ecological contexts simply by being in different places. As noted earlier, ecological differences can affect the trajectory of premating sexual selection in two broad ways, via natural selection on sensory systems or via signal transmission [11,13]; the former is more likely to lead to reproductive isolation than the latter. In secondary contact, populations spatially overlap, and the degree to which they have diverged into unique ecological niches may be more critical for persistence than the degree to which they have diverged in sexually selected traits. Finally, disruptive selection into distinct ecological niches appears to be a defining feature of sympatric speciation [66]. The correlated evolution of magic traits might be necessary for sexually selected traits to evolve in speciation with gene flow; even here, some magic traits, such as a tendency to mate on a host plant, are not sexually selected, and assortative mating evolves as a byproduct of disruptive natural selection rather than sexual selection [83].

Genomic context

Genomic context refers to the genomic architecture of the trait(s) associated with sexual selection (e.g., effect size, pleiotropy, epistasis, mutation and recombination rates), which is then manifest in the pattern and degree of population genomic differentiation. Genomic advances of the past 20 years have validated the 'genic view' of speciation [84], showing that divergence during speciation is heterogeneous across the genome [85,86]. Current research explores how the spatial, temporal, and ecological contexts of speciation interact with genomic architecture in driving speciation [85,86]. Pleiotropy of sexual signals and preferences is arguably the most conducive

genomic architecture for speciation by sexual selection [83,87], and work over the past 20 years by Shaw and colleagues on Hawaiian crickets (*Laupala* spp.) provides a potentially compelling example [88–90]. Another exciting new study provides evidence of how sexual selection shapes genomic divergence during speciation; lines of *Drosophila* subjected to varying sexual selection intensity showed 'islands' of divergence, especially on the X chromosome, with evidence of selection in many islands [91].

Importantly, not all diverging populations will experience all spatial contexts; many taxonomically 'good', allopatric species will never demonstrate reproductive isolation from their sister [5,73,92]. Many such allospecies differ markedly in mating signals, suggesting that sexual selection has driven phenotypic divergence; however, whether sexual selection has driven speciation depends on the species concept being applied. A strict biological species concept would require evidence of reproductive isolation to implicate sexual selection, or any evolutionary mechanism, as causal. A recent survey of species concept usage found that practicing biologists differ in their adherence to the biological species concept, largely depending on their specific discipline and the timescale of their question [93]. We suggest that an inclusive understanding of the contribution of sexual selection to speciation should be flexible enough to accommodate a range of species concepts.

Concluding remarks

The past 20 years has led to tremendous progress in our understanding of speciation and the role of sexual selection. To reflect that progress, we suggest an updated perspective for studying the role of sexual selection in the process of speciation: sexual selection contributes to speciation when a change in heritable phenotype(s) that affect mating or fertilization success within a population leads to two or more distinct forms separated by geographic or reproductive barriers. The role of sexual selection in speciation is influenced by variation in spatial, temporal, social, ecological, and genomic contexts.

This updated perspective reflects progress in the field in three ways. First, it redefines the mechanism of sexual selection from a 'parallel change in mate preference and secondary sexual traits' to one that encompasses any trait evolving by any mechanism of sexual selection [i.e., heritable phenotype(s) that affect mating or fertilization success]. Second, by excluding the original closing clause 'and when this is the primary cause of reproductive isolation', it acknowledges the interaction of natural and sexual selection in species formation. Sexual selection contributes to speciation whether or not it interacts with natural selection; thus, restricting our understanding of speciation by sexual selection to cases in which prezygotic isolation due to divergent sexual selection is the primary cause of reproductive isolation would likely underestimate its contribution to speciation. Third, it allows species to be defined by geographic *or* reproductive barriers, acknowledging the reality of species taxonomy, the various use of species concepts across biology, and the importance of evolutionary processes in early divergence. As we celebrate the 150th anniversary of *The Descent of Man* [6] and the 20th anniversary of Panhuis *et al.* [2], we hope that this updated perspective on the role of sexual selection in speciation inspires the next generation of researchers to take on, and to generate their own, outstanding questions in the field (see Outstanding questions).

Outstanding questions

Do different mechanisms of sexual selection make range expansion and coexistence more or less likely?

How do different mechanisms of sexual selection interact with social and ecological context during the evolution and maintenance of population differences?

In what ecological and social contexts do mate preferences tend to diverge?

What are the relative contributions of sexual and natural selection to the evolution and maintenance of population divergence in different spatial contexts?

When populations first become geographically isolated, which traits diverge first and in what ecological contexts?

What is the relative importance of time since divergence and ecology in the maintenance of reproductive boundaries during range expansion?

Are there differences in the genomic architectures of sexual traits that are associated with population divergence? Are sexual traits with simple genomic architecture more likely to be involved in rapid population divergence?

Are different mechanisms of sexual selection more or less likely to drive speciation 'alone' (i.e., independent of ecological differences)?

Declaration of interests

None declared by authors.

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