

# The contribution of sexual selection to ecological and mutation-order speciation

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Abundant evidence supports a role for sexual selection in the evolution of reproductive isolation, and it is thus unsurprising that much attention has been given, both conceptually and empirically, to understanding its role in speciation. In doing so, debate has arisen on how sexual selection fits within the much used ecological versus mutation-order classification of speciation mechanisms, with sexual selection often presented as a distinct third alternative. We argue that models of speciation by sexual selection include a fundamental role of divergent selection between environments or mutation order in initiating the process. Rather than representing a unique mechanism, sexual selection layers a coevolutionary process between males and females on top of the classic mechanisms such that the evolution of each sex can now be driven by divergent selection, mutation order, and selection arising from interactions with the other sex. In addition to blurring the distinction between ecological and mutation-order speciation, this coevolutionary process is likely to speed divergence. Sexual selection is not unique in this way; coevolutionary processes can similarly arise from ecological interactions between populations or species, with similar results. Ultimately, understanding the contribution of sexual selection to speciation will require identifying the processes that drive the divergence of mating biases.

**KEY WORDS:** Coevolution, ecological speciation, mutation order, reproductive isolation, sexual isolation.

Under the biological species concept, speciation is the process by which barriers to gene flow, often termed reproductive isolation, evolves (Mayr 1963; Coyne and Orr 2004). Mechanisms of speciation are commonly divided into two main classes: ecological and mutation order (Schluter 2009), and this distinction is most relevant early in the speciation process. Ecological speciation describes a process in which the evolution of reproductive isolation results from adaptation to different environments or niches. Natural selection is divergent (or disruptive) in that alleles that are advantageous in one environment or niche are not in the other. In contrast, under mutation-order speciation the evolution of reproductive isolation is ultimately tied to the chance occurrence and fixation of different alleles in different populations. While the fixation of these allele can occur by drift alone, natural selection may also be involved, although in such cases selection is not divergent between environments or niches in that the mutations that fix in one population would also be advantageous in the other.

Sexual selection, on the other hand, is a process that occurs when variation in a trait is associated with differences in mating (or fertilization) success, or in other words, when one or more traits bias the outcome of mate competition toward certain male phenotypes (Andersson 1994). Such biases can arise from male-male competition (i.e., intrasexual selection), including pre- and postcopulatory processes like male combat, scramble competition, and sperm competition, and from female choice (i.e., intersexual selection), again including pre- and postcopulatory processes such as mate preferences/female resistance and cryptic female choice. Given that reproductive isolation defines the speciation process, it seems likely that selection arising from variation in mating success will often be involved. Consistent with this, an important role for sexual selection in speciation is inferred because male secondary sexual traits and genitalia tend to evolve rapidly, are often the most divergent phenotypes among closely related taxa, and tend to be spectacularly diverse among species in several of the most iconic adaptive radiations (Eberhard 1985;

Arnqvist 1998; Schluter 2000). In addition, behavioral isolation (also known as sexual isolation) is a reproductive barrier that exists when individuals from different populations are less likely to court or accept one another as mates. Behavioral isolation is often the most important reproductive barrier between closely related species (Mayr 1963; Coyne and Orr 2004) and sexual selection, because it generates mating biases, is thought to be central to its evolution.

The binary classification of ecological versus mutation-order speciation mechanisms was not proposed with sexual selection in mind, and this has caused more than a little debate about how sexual selection fits within it. The observations summarized above have led to a widespread opinion that sexual selection is a third mechanism of speciation in and of itself, representing an alternative process by which reproductive isolation can evolve that is distinct from ecological and mutation-order speciation (Panhuis et al. 2001; Safran et al. 2013). Likewise, there has been considerable discussion about the potential for interactions between sexual selection and ecological speciation (Ritchie 2007; Sobel et al. 2010; Maan and Seehausen 2011; Martin and Mendelson 2016; Servedio and Boughman 2017). But can sexual selection initiate the evolution of reproductive barriers in a way that is not ultimately caused by divergent natural selection between environments or the chance occurrence of different mutations? We argue the answer to this question is—no.

Although there are many ways in which sexual selection can contribute to the evolution of reproductive isolation, and while much attention has been given to identifying these, in all cases the initial evolution of reproductive barriers involves a fundamental contribution of divergent selection arising from differing ecologies and/or a mutation-order process (Schluter 2001). For example, in systems where divergent mating biases (e.g., female choice/resistance) are associated with speciation, the mate biasing mechanism will have evolved initially either because of mutation-order effects or divergent natural selection between environments. Consider the divergent evolution of mating biases in three of the most commonly considered scenarios of speciation involving sexual selection:

### 1) *Sexual conflict*

In polygamous species, where there is conflict over mating rate, traits may evolve in females that reduce mating rate, and these resistance traits will favor traits in males that counter their effect (Arnqvist and Rowe 2005). In allopatric populations, different alleles resulting in different adaptive resistance phenotypes may arise and fix. These different phenotypes will favor different male mating traits, and the resulting phenotypic divergence may cause reproductive isolation (e.g., behavioral isolation, intrinsic genetic incompatibilities) upon secondary contact (Rice 1998).

This is a form of mutation-order speciation. Alternatively, the traits underlying sexual conflict may also be targets of natural selection and may diverge in association with ecology (Arbuthnott et al. 2014). If any reproductive isolation occurs as a by-product of such divergence, this would be a form of ecological speciation.

### 2) *Direct selection on mate preferences*

In these models, alleles affecting mate preferences also alter an individual's fitness directly (Kirkpatrick and Ryan 1991; Coyne and Orr 2004). In most such models, preferences diverge because of differences in the direct cost or benefit of their expression in terms of female nonsexual fitness (i.e., viability or fecundity), or in other words, due to differences in natural selection between environments, making this a form of ecological speciation. A simple example is when a preference evolves because of natural selection on the sensory system (i.e., sensory bias), and natural selection differs between two allopatric populations, causing different preferences and thus leading to reproductive isolation (Boughman 2002). The contribution of sexual selection to speciation in such models is often over emphasized, as it is divergent natural selection that is ultimately responsible for preference divergence.

### 3) *Indirect selection on mate preferences*

In these models, preferences diverge because they are genetically correlated with a character under divergent selection (Kirkpatrick and Ryan 1991; Coyne and Orr 2004). The key to these models therefore concerns the mechanism underlying divergent selection of this other character. There is a variety of ways in which this can occur. In a good-genes scenario, for example, higher genetic quality males produce more attractive displays and, by preferentially mating with such males, a correlation develops between genes for female preference and those conferring high nonmating fitness. Divergence can occur because mutation-order effects and/or divergent ecologies cause different characters to signal high nonmating fitness in males in separate populations, and females would then be favored to prefer their own (i.e., local) males (Schluter and Price 1993; Mendelson et al. 2014). These would be examples of mutation-order and ecological speciation respectively. Indirection selection on preferences also arises from their genetic correlation with the male display they target. Referred to as a Fisher process, males expressing a preferred trait have a mating advantage over other males and, because of the genetic correlation that necessarily develops between genes for a preference and those for the preferred trait, a self-reinforcing process can result (Fisher 1930). Like with a good-genes scenario, both mutation-order and ecologically divergent selection can lead to population divergence under a Fisher process (Lande

1981; Pomiankowski and Iwasa 1998), making these examples of mutation-order and ecological speciation, respectively.

In all of the above cases, the first step in the evolution of reproductive isolation is a change in mating biases due to either mutation-order effects or natural selection (direct or indirect) on that bias. So, if sexual selection is not an independent mechanism for the evolution of reproductive isolation, as we have argued above, how does it map onto the ecological versus mutation-order classification? One possibility is that when sexual selection is involved, the speciation process can be unambiguously designated as either ecological or mutation-order, as the examples above seem to suggest. An alternative is that the ecological versus mutation-order distinction does not work well when sexual selection is involved. We argue the latter will often be the case.

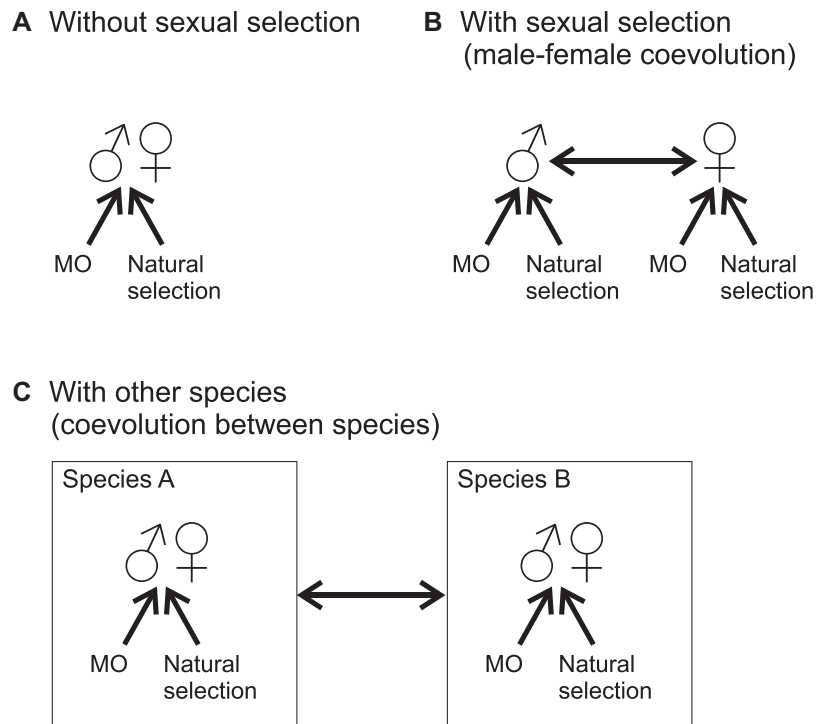
When sexual selection is involved, a key distinction from the traditional binary classification is the addition of a coevolutionary process between males and females within each population. The impact is threefold; first, the fact that it is a coevolutionary process means there is an additional force of selection at play (e.g., female preference; Fig. 1A vs 1B) such that divergence involves not just ecological selection and/or mutation-order effects in each population, but also subsequent reciprocal evolutionary change between the sexes within each population. Second, with two entities involved (i.e., males and females), the binary ecological versus mutation-order distinction is likely to become blurred. For example, although natural selection may explain divergence on one side of the process (say preferences), mutation-order effects may underlie the response of the other side (say, male traits; Fig 1B). This is likely to further complicate problems with unambiguously assigning even the early stages of a speciation process to a particular mechanism. Third, in addition to blurring the distinction between ecological and mutation-order speciation, the coevolutionary process that results from sexual selection can quickly exaggerate any initial evolution no matter what the cause, thereby facilitating much more rapid divergence. This acceleration occurs because evolutionary change in one sex, no matter what the cause, is likely to alter selection on the other sex. This is almost certainly why traits involved in coevolutionary processes, like sexual signals and displays and male and female genitalia, are the most divergent among closely related taxa. Because the distinction between ecological and mutation-order speciation can break down as divergence proceeds (Schluter 2009), an acceleration of divergence is likely to exacerbate this issue, meaning that when sexual selection is involved, speciation may be more rapid and the initial cause thus harder to infer. In sum, in the presence of sexual selection, the sexes coevolve with each driving evolution in the other. Each sex can therefore be affected by mutation-order, natural (ecological) selection, and selection resulting from interactions with the other sex. Importantly, the coevolutionary process resulting from the interaction of the sexes can easily

recruit either mechanism (i.e., mutation-order and ecological selection) such that trait divergence initiated by one can quickly involve the other, and divergence itself is likely to be accelerated.

The additional involvement of a coevolutionary process could arguably be used to define speciation by sexual selection as a process distinct from mutation-order or ecological speciation. However, other coevolutionary processes may also affect population divergence, and hence speciation, in systems that are unaffected by sexual selection. For example, coevolution can also occur between species (Fig. 1C) and traits involved in this coevolution are similarly likely to diverge rapidly under the joint influences of mutation-order and divergent ecological selection, thereby promoting speciation. Indeed, between-species coevolution has long been seen as a major driver of diversification in insect herbivores and their host plants, and flowering plants and their pollinators (Ehrlich and Raven 1964; Thompson 1994; Althoff et al. 2014). If one or both of two interacting species were also evolving via sexual selection, then the scenario would be even more complicated given two coevolutionary processes at play with potential contributions of divergent selection and mutation-order to each of the coevolving units.

In the end, it appears that mutation-order and divergent natural selection retain their primacy in understanding the early stages of divergence that initiate speciation. However, coevolutionary processes, both between the sexes and between species, add one or more layers of complexity because there are interacting entities, each potentially exerting selection on the other, and each susceptible to mutation-order effects and divergent natural selection. These added layers clearly make assigning early divergence to either mutation-order or divergent selection problematic, as it may be both, and the potential speed of the process threatens to rapidly obscure this history. It is well recognized that, as speciation proceeds, it becomes increasingly difficult to identify the mechanism that initiated divergence, and this problem is likely to be exaggerated for those traits involved in a coevolutionary process. A signal of parallel evolution/speciation, a pattern often used to infer ecological speciation (Schluter 2000), will thus be easier to detect earlier during divergence (because the likelihood of mutation-order coming into play will increase as divergence proceeds) and it will persist longer for traits not involved in a coevolutionary process.

What then do we do with this perspective on sexual selection and speciation? First, we think it is prudent to drop the practice of considering sexual selection a third speciation mechanism, on par with mutation-order and divergent selection. Instead, it and other coevolutionary processes should be viewed as additional, complicating layers, set atop of the two traditional mechanisms. In systems in which sexual selection is implicated, we should focus on how mutation-order and/or divergent natural selection have contributed to a divergence in mating biases, and the favored traits



**Figure 1.** Three scenarios depicting the processes affecting the evolution of reproductive isolation. (A) The traditional binary classification of speciation mechanisms in which reproductive isolation evolves ultimately due to natural selection adapting populations to different environments or the chance occurrence and fixation of different mutations in different populations (mutation order, MO). (B) The addition of sexual selection allows divergent selection and mutation-order effects to independently affect change in each sex, and causes an intersexual coevolutionary process to overlay these classic mechanisms. (C) Likewise, the addition of a coevolutionary process between species (e.g., host-parasite, plant-pollinator, etc.) can similarly blur the role of the classic processes, each of which can affect change in each of the coevolving units.

of those biases. In most cases, we expect that it will be the mating biases that evolve first, with the preferred traits following. If correct, this requires a focus on the forces shaping preferences and other mating biases. As a research program, this repeats a long-standing call in the sexual selection literature (e.g., Kirkpatrick and Ryan 1991; Kirkpatrick and Barton 1997; Kokko et al. 2003; Arnqvist and Rowe 2005), upon which progress has been very slow. It is usually easy to understand the exaggeration of preferred traits—they are preferred—but extremely difficult to understand the spread of a preference. Although we suspect that traits will follow preference, one can imagine it occurring the other way around.

In summary, much of the interest in sexual selection has arisen from that the fact that the coevolutionary process it generates leads to rapid and diversifying evolution, an outcome it shares with other coevolutionary processes. It is this that also makes sexual selection so interesting for those that study the origin of species. Sexual selection can be accommodated within the established framework of ecological and mutation-order speciation, although it is likely to blur the distinction between these and to make it more challenging to infer the process that initiated divergence. In the end, understanding sexual selection's

contribution to speciation requires knowing whether reproductive isolation involves mating biases, and if so, determining the role of mutation-order and/or divergent selection between environments in the evolutionary divergence of these biases.

#### AUTHOR CONTRIBUTIONS

H.D.R. and L.R. both conceived the ideas/opinions and cowrote the manuscript.

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