

Sexual Selection and Speciation

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Abstract

Sexual selection favors traits that give the bearer an advantage in attracting high-quality mates or competing for them. Such traits can contribute to prezygotic isolation between populations, which is thought to usually be the first step toward speciation. Theoretical and empirical research suggests that the prospects for speciation are enhanced when sexual selection operates in conjunction with other evolutionary processes, such as niche divergence and reinforcement. Case studies at the genus level have yielded the most compelling evidence for causal links between sexual selection and speciation. Future research priorities are discussed in this article.

Keywords: Intrasexual competition; Mate choice; Mate preference; Mate recognition; Reinforcement; Reproductive isolation; Secondary sexual character; Sensory drive; Sexual conflict; Sexual selection; Speciation

Key points:

- Sexual selection has the potential to cause new species to form rapidly.
- Several such mechanisms have been proposed but only a few have been validated with formal theory.
- Mechanisms that involve ecological divergence may be more likely to cause speciation than those only involve shifts in mate preferences or secondary sexual characters.
- Comparative studies of the relationship between speciation rates and indices of sexual selection have yielded conflicting results.
- Case studies of individual species or genera have provided clear evidence for several sexual selection-speciation mechanisms.

- Other case studies have shown how sexual selection can oppose speciation.
- Laboratory evolution experiments have had mixed results but hold promise for testing and refining theory.
- Conservation relevance: some species are being lost to hybridization because anthropogenic pollution interferes with mate choice.

Introduction

Sexual selection was Charles Darwin's solution to the existence of secondary sexual characters, such as the ornate plumage of male birds of paradise, the exaggerated weaponry of male horned beetles, and the elaborate antennae of male gypsy moths (Darwin, 1871; Andersson 1994). These traits were puzzling, precisely because they seemed costly for survival. Darwin's explanation was that such traits evolve in spite of their survival costs because they increase male mating success. He proposed that male ornamentation evolved in response to female mate choice, that male weaponry evolved because of contest competition among males for access to females, and that enlarged male sensory organs evolved because of scramble competition for females.

Sexual selection by female choice, arguably Darwin's most controversial idea, was criticized by several prominent evolutionists, including Alfred Russell Wallace. Darwin himself seemed unable to explain why females should prefer ornamented males. Ronald Fisher (1930) outlined the basic explanations that are widely accepted today, but it took another 50 years for these ideas to be formally modeled and tested empirically. In the meantime, sexual selection was supplanted by the notion that secondary sexual characters are reproductive isolating mechanisms, that is, traits that prevent interbreeding between closely related species.

These two ways of thinking about secondary sexual characters were formally united in the 1980s. Mathematical models by Russell Lande (1981) and other evolutionary theorists showed how sexual selection, in combination with genetic drift or ecological gradients, could cause populations to diverge in mate preferences and secondary sexual characters to the point of reproductive isolation. Research on sexual selection exploded in the 1980s, but with few exceptions, mate recognition between species and mate choice within species continued to be treated as separate phenomena. After the first wave of studies established the ubiquity of female choice, finally vindicating Darwin, the primary focus of empirical research became to test the assumptions behind several alternative models of mate preference evolution. Empirical research on the role of sexual selection in speciation was uncommon until the last few years of the 20th century.

Since speciation was studied for decades without any explicit consideration of sexual selection (Coyne and Orr, 2004), it is worth asking whether taking sexual selection into account is really necessary. Ultimately, this is an empirical question. It would be hard to deny that sexual selection is at least partly responsible for the extraordinarily high rates of speciation in African lake cichlid fishes, in which some closely related species differ only in male coloration and female color preferences, or in Hawaiian crickets, in which morphologically indistinguishable sister species differ in male song and female song preferences. Exactly what role sexual selection has played in the radiation of these and other taxonomic groups is a very active area of research (Mendelson and Safran 2021).

Processes Linking Sexual Selection and Speciation

What distinguishes sexual selection from most other evolutionary processes is its potential to cause rapid prezygotic or behavioral isolation. Although sexual selection can also increase postzygotic isolation by reducing the mating success of hybrids, this requires some degree of prezygotic isolation. We, therefore, restrict our attention here to processes leading to prezygotic isolation (with or without postzygotic isolation).

Whether a given mode of speciation is viewed as driven by sexual selection depends on how narrowly the term sexual selection is interpreted. Strictly speaking, sexual selection refers to covariation between traits and mating success, where mating success includes the quantity or quality of mating partners. However, mate preferences and secondary sexual characters can also evolve in response to other forms of natural selection, with potentially similar consequences for reproductive isolation and speciation. If mate preferences and secondary sexual characters are genetically correlated (as assumed under some sexual selection models), then selection on one could generate a correlated response in the other. For example, if geographic variation in predation intensity affected the survival cost of a secondary sexual character, that could cause populations to diverge in both the secondary sexual character and a genetically correlated mate preference, potentially resulting in reproductive isolation between populations. Theoreticians have tended to focus on speciation via sexual selection in the strict sense, but most empirical studies (especially comparative studies) are unable to identify the specific mechanisms of selection. More to the point, there are many possible causal links between sexual selection and speciation, and the ones that have captured the attention of theorists may not be the most prevalent in nature.

At least eight processes could contribute to prezygotic reproductive isolation by causing population divergence in secondary sexual characters and mate choice (see Table 1). Of these, only reinforcement represents direct selection for reproductive isolation; under the other processes, reproductive isolation emerges as a byproduct. Reinforcement can be viewed as a form of good genes sexual selection, where members of the other population represent low quality mates (i.e., hybrid offspring have low fitness), but it is usually treated separately from sexual selection. In reinforcement models, sexual selection can be side-stepped by assuming the existence of a single assortative mating (“like mates with like”) locus, although it is probably more realistic to model mate preference and secondary sexual character loci separately. Aside from reinforcement, Fisherian selection and sexual conflict have received the most theoretical attention. The remaining processes listed in Table 1 represent relatively unstudied links between sexual selection and speciation that probably deserve greater attention. None of these processes is mutually exclusive; multiple processes operating together may be more likely to cause speciation than any single process.

Not all instances of divergence in secondary sexual characters and mate preferences are equally likely to cause speciation. Asymmetrical mate preferences, in which females of one population mate assortatively (i.e., prefer males from their natal population), while females from the other population mate indiscriminately, are likely to cause asymmetrical gene flow but not reproductive isolation. Likewise, shifts in secondary sexual characters that are not accompanied by corresponding shifts in mate preferences are unlikely to cause reproductive isolation (e.g., males from the population with the most elaborate version of the character may simply be preferred by females from both populations). In general, shifts in sexual traits or mate preferences alone seem unlikely to cause speciation. Consequently, most theoretical work has

focused on mechanisms that are capable of driving populations apart in mate preferences and sexual traits simultaneously.

Mathematical Models of Speciation by Sexual Selection

Most models of speciation by sexual selection are based on Lande's formalization of Fisher's insight that both sexes carry genes that influence the expression of mate preferences and secondary sexual characters (process 3 in Table 1). Females with a strong preference for, say, long-tailed males, tend to produce offspring with genes for both long tails and the long-tail preference. This can result in a positive feedback loop in which mate preferences and secondary sexual characters coevolve in unpredictable ways, potentially leading to reproductive isolation between allopatric populations. Populations can diverge by drift alone, but the prospects for speciation are enhanced when populations occupy different positions along an environmental gradient that influences the survival costs of the secondary sexual character.

Under some circumstances, Fisherian sexual selection could result in sympatric speciation. This has been the subject of several modeling efforts. A frequent conclusion is that sympatric speciation is more likely when Fisherian selection is coupled with ecological (niche) divergence that affects the selective optimum or expression of the secondary sexual character (e.g., van Doorn *et al.*, 2009). However, Fisherian selection can also cause ecological divergence to break down after gene flow is established between formerly allopatric incipient species (Servedio and Bürger, 2014). Based on recent models, Maria Servedio (2016) concluded that Fisherian selection actually undermines the speciation process, under most circumstances.

Models by Sergey Gavrillets and colleagues (Gavrillets and Hayashi, 2005; Gavrillets, 2014) suggest that the sexual conflict mode of sexual selection may be particularly likely to result in speciation (process 4). In these models, mating is costly for females (above some optimal mating rate) and female preferences arise from resistance to mating. Males evolve adaptations to overcome female resistance and females evolve counteradaptations. Allopatric populations can rapidly diverge to the point where males are unable to mate with females from another population, resulting in reproductive isolation. Speciation is not an inevitable outcome, however; males from one population could be superior at mating with females from both populations (asymmetric preference). Sexual conflict can also cause sympatric speciation if females evolve two alternative strategies for resisting mating and males evolve adaptations for specializing on one type of female or the other, but the likelihood of this outcome is unclear.

The sobering message from theoretical work is that many different outcomes are possible, even within the relatively small subset of parameter space that has been explored so far. Still, it may be possible to parameterize models for particular systems to evaluate whether speciation is a likely outcome. Future theoretical work could also clarify which assumptions of the models most strongly affect the prospects for speciation.

Empirical Evidence

Overview

A wide range of data has been put forth as evidence that sexual selection plays a role in speciation. Here, we review three categories of evidence: taxonomically broad comparative studies (family level or above), case studies of smaller taxonomic scale, and experimental evolution studies.

Broad Comparative Studies

Several published studies correlating species richness with putative indices of sexual selection (e.g., sexual dimorphism, degree of polygyny, size of testes) have found positive correlations, after controlling for phylogeny. Similar studies, however, have found no correlations or even negative correlations. Positive correlations suggest that sexual selection increased speciation rates or decreased extinction rates. It has long been recognized that the demographic effects of sexual selection (e.g., reduced effective population size) could increase extinction rates. Hence, positive correlations have usually been taken as evidence that sexual selection increased speciation rates. But recent theoretical studies have shown that some forms of sexual selection can increase population mean fitness sufficiently to override the demographic effects and reduce extinction rates (e.g., M'Gonigle et al. 2012; Martinez-Ruiz and Knell 2017). Another important caveat is that indices of sexual selection might correlate with other factors that affect species richness. Taxonomy is often based on male secondary sexual characters and allopatric populations are more likely to be classified as separate species if they differ in such characters. Thus, species richness might be systematically overestimated in clades with elaborate genitalia or conspicuous coloration. Consequently, using sexual dimorphism in such traits as an index of sexual selection is problematic, and to the extent that other indices of sexual selection correlate with sexual dimorphism, they might suffer from the same problem. Another reason to be leery is that similar studies on the same taxonomic groups (e.g., birds) have yielded contradictory results (reviewed by Ritchie, 2007; Cally et al. 2021).

In the most recent and largest comparative study of sexual selection and speciation in birds, Justin Cally and colleagues (2021) found that (a) sexual dichromatism, which is widely used as an index of sexual selection in birds, was not predictive of speciation or extinction rates in a dataset that included 97% of passerine species ($n = 5812$), and (b) sexual size dimorphism was predictive of speciation rates in a dataset with 58% of passerine species ($n = 2465$). These results were interpreted, respectively, as evidence that (a) sexual dichromatism might not be a good index of sexual selection after all, and (b) male-male competition might be the mechanism driving high speciation rates in birds.

The only broad comparative study specifically designed to test the hypothesis that intrasexual competition (process 5) contributes to speciation yielded negative results. Zachary Emberts and John Wiens (2021) used data on 45851 species from three major insect clades to test whether male-male competition increases the net diversification rate (i.e., speciation minus extinction). Species were classified according to whether males possess sexually selected weaponry, i.e., morphological structures that were known or suspected to be used in male-male contests over mating opportunities (e.g., horns, enlarged femurs). In all three clades, lineages with and without sexually selected male weaponry had similar rates of speciation and extinction, leading to the inference that male-male competition does not affect the net diversification rate. As the researchers note, however, this conclusion applies only to precopulatory male-male competition, which seems unlikely to drive speciation without a concurrent shift in female preferences or mating opportunities.

In many insect taxa, males compete to fertilize eggs during or after copulation using mechanisms (behavioral, mechanical, chemical, etc.) that reduce female fitness, resulting in sexual conflict, which in theory could increase the rate of allopatric speciation. Göran Arnqvist and colleagues (2000) tested this prediction by comparing lineages in which females typically mate with multiple males (polyandry) to those in which females typically mate with a single male (monandry). As predicted, species richness was usually higher in the polyandrous lineages;

overall, the speciation rate was estimated to be four times higher than in monandrous lineages. Nevertheless, subsequent comparative research on a range of taxa and taxonomic scales has produced mostly negative results; indices of sexual conflict have only rarely been found to be associated with rates of speciation (Gavrilets 2014; Carvalho et al. 2021).

The comparative studies reviewed so far relied on indices or proxies of sexual selection (e.g., sexual dimorphism, mating system), each of which has potential drawbacks (reviewed in Janicke et al. 2018). As an alternative approach, Tim Janicke and colleagues (2018) mined the literature for estimates of selection metrics from population studies and carried out a phylogenetic analysis across diverse animal taxa (e.g., flatworms, vipers, humans). Two of nine metrics emerged as significant positive predictors of species richness at the family level: the difference between the sexes in the total opportunity for selection (defined as the variance in reproductive success) and the male Bateman gradient (defined as the regression slope of male reproductive success on male mating success). These results were interpreted as clear support for the hypothesis that sexual selection promotes speciation.

On the lower end of the taxonomic scale for large comparative studies, Nathalie Seddon (2005) used data on song and morphology of 163 species of antbirds (Thamnophilidae) to test predictions of the reinforcement, local adaptation, and pleiotropy hypotheses (processes 2, 6 and 7). All three hypotheses received some support. Pitch and temporal patterning of songs correlated with body mass and bill size, respectively, as predicted from biomechanical constraints on song production (i.e., pleiotropy). Pitch also correlated with acoustic transmission properties of the forest strata in which antbirds typically sing, as predicted by the acoustic adaptation hypothesis. Finally, closely related sympatric species differed more in song than closely related allopatric species, providing evidence for reinforcement or post-speciation reproductive character displacement. However, the latter result could also be explained by age differences between sympatric and allopatric lineages. Sympatric lineages might differ more in sexual characters because they are older, on the average, than allopatric lineages (Tobias *et al.* 2014).

Case Studies

African lake cichlids

Cichlid fishes in the lakes of East Africa have become an iconic example of speciation by sexual selection. In Lake Victoria, for example, over 500 species appear to have evolved from a few ancestral species in the past 100,000 years. Many of the species differ primarily in male coloration and are genetically isolated from each other only by female preferences. Hybrids are viable, fertile, and intermediate in coloration. Some species contain multiple male color morphs and color morph-specific female preferences, and may be in the process of speciating yet again. Although several models of speciation have been loosely based on this system, it would be wrong to infer that we understand how speciation occurs in the African lake cichlids themselves. How color polymorphisms arise and how they are maintained long enough for reproductive isolation to evolve, is largely an unsolved mystery. One solution proposed by Ole Seehausen and Dolph Schluter (2004) is that intrasexual (male–male) competition over breeding territories (process 5) favors rare color morphs, setting the stage for the evolution of morph-specific mate preferences and reproductive isolation. Several indirect lines of evidence support this hypothesis, and aggression biases favoring rare male color morphs have been documented in several species. An alternative hypothesis is that the color divergence is a product of small-scale differences between species in breeding habitat, coupled with sensory drive (process 6; Endler 1992). Water

color is red-shifted (i.e., shifted toward long wavelengths) at greater depths, and thus, different colors are conspicuous at different depths. In one sympatric species pair, the species in which males are typically yellow and red (*Pundamilia nyererei*) breeds at greater depths than the species in which males are typically blue (*Pundamilia pundamilia*) (Fig. 1), and females use male color to mate assortatively by species. In optomotor tests, female *P. nyererei* are more sensitive to red light and female *P. pundamilia* are more sensitive to blue light. These species differences in wavelength sensitivity can be largely explained by sequence divergence in genes coding for visual pigments (opsins). Seehausen et al. (2008) proposed a complex verbal model of the speciation process that includes sensory drive, Fisherian selection, gene flow, and reinforcement.

Intrasexual competition might have played a central role in the evolution of partially reproductively isolated ecomorphs of the cichlid fish *Telmatochromis temporalis* (Winkelman et al. 2014). In the littoral zone of Lake Tanganyika, the ‘rock’ ecomorph is found in rocky areas and the ‘shell’ ecomorph is found primarily in shell beds. Aquarium experiments showed that males of both ecomorphs preferred rocky habitat in the absence of competitors, but in the presence of the ‘rock’ ecomorph, males of the smaller ‘shell’ ecomorph shifted to shell habitat. Females did not prefer to associate with males of their own ecomorph, which suggested that reproductive isolation is maintained by habitat segregation arising from male-male territory competition (Winkelman et al. 2014). This is among the clearest examples of how intrasexual competition alone could initiate speciation. Reinforcement would probably be required to complete the process.

Greenish warblers

Greenish warblers (*Phylloscopus trochiloides*) provide another example of how intrasexual competition might cause populations to diverge in ways that lead to speciation. In a study of three parapatric populations, Elizabeth Scordato (2018) found evidence that female choice consistently favored males with longer songs, while shorter songs were more effective in male-male territorial interactions. Average song length correlated negatively with population density (a proxy for the strength of male-male competition), suggesting that selection arising from male-male competition has caused song length to diverge between populations. This is a ring species, and populations in the secondary contact zone are reproductively isolated. Scordato (2018) proposed that interactions between male-male competition, female choice, and habitat quality had cascading effects that culminated in reproductive isolation in the contact zone.

Jacanas

Intrasexual competition also has the potential to undo speciation by overcoming reproductive barriers between species. One example of how that might happen was found in the hybrid zone between Northern and wattled jacanas (*Jacana spinosa* and *J. jacana*, respectively) in Central America. These shorebirds exhibit ‘sex-role reversal’, with polyandrous females competing for territories that can encompass the territories of multiple males (Lipshutz et al. 2019). A difference in the competitive ability of females of the two species appears to account for asymmetrical introgression of mtDNA and genes that influence body size (Lipshutz et al. 2019). The species have converged in body size in the hybrid zone, but steep clines in genomic markers and plumage indicate that hybrids have low fitness (Lipshutz et al. 2019). Thus, intrasexual competition and reinforcement appear to work in opposite directions in this case.

Poison dart frogs

Another way that intrasexual competition could oppose speciation is by overriding female choice. Strawberry poison dart frogs (*Oophaga pumilio*) occur in several color morphs, and females prefer males of the same color morph as themselves, while males are more aggressive toward males of their own morph. The same combination of color-based female choice and male aggression biases has been proposed to promote speciation in African Lake cichlids (see above). However, when female frogs were placed in terraria with males of two different color morphs, the female usually mated with the dominant male, regardless of which male was of her color morph (Yang and Richards-Zawacki 2021).

Hawaiian crickets

Crickets in the endemic Hawaiian genus *Laupala* have the highest speciation rate on record for arthropods. Closely related *Laupala* species are morphologically and ecologically indistinguishable and can produce viable hybrids. The only conspicuous difference between sympatric species is that they differ in the pulse rate of male courtship song. Tamra Mendelson and Kerry Shaw (2005) found that female *Laupala* can discriminate between conspecific and heterospecific song from a distance and preferentially approach conspecific males. This suggested that correlated divergence in song and song preferences drove speciation, but further research revealed a more complex story (Mullen et al., 2007). In a laboratory study of two allopatric species, conspecific courtship sequences usually went to completion, while heterospecific courtship rarely proceeded to the stage where males provide spermatophores. However, when females of the same species were paired with F2 hybrid males, which vary widely in song pulse rate, the song pulse rate of the males did not predict whether courtship proceeded to completion. A possible explanation is that chemical or tactile cues are exchanged between the sexes during courtship and that divergence in such cues, not courtship song, is responsible for the breakdown in heterospecific courtship at close range. In support of this explanation, the researchers found evidence for rapid divergence between *Laupala* species in cuticular hydrocarbon (CHC) profiles. Whether species differences in CHCs contribute to reproductive isolation in *Laupala* remains to be determined. Research on this system has continued to focus on the role of song divergence in speciation (Mullen and Shaw, 2014; Xu & Shaw 2021).

Threespine stickleback

Sexual selection and ecological character displacement both appear to have played integral roles in the diversification of threespine stickleback. In the lakes of British Columbia, Canada, these fish occur in two ecologically and morphologically distinct species pairs: a larger benthic ecotype that forages in the littoral zone, and a smaller limnetic ecotype that forages in open water. Limnetic and benthic ecotypes within a lake are more closely related to each other genetically than they are to fish of the same ecotype in different lakes, probably because each lake was colonized independently by the marine ancestor (*Gasterosteus aculeatus*). Nevertheless, benthics and limnetics within a lake are reproductively isolated, while fish of the same ecotype from different lakes are not. This suggests that the same prezygotic isolating barriers arose independently in different lakes. Indeed, Janette Boughman and colleagues (2005) found that male coloration and female sensitivity to red light differed between ecotypes in the same direction in three different lakes. Compared to benthics, limnetic males have more red and less black coloration, and limnetic females are more sensitive to red light. In each lake, reproductive

isolation between ecotypes appears to be maintained by female choice based on male size and color. The consistent direction of the differences between ecotypes in male color and female sensitivity to red light suggests that they are caused by habitat differences (albeit in the opposite direction as seen in African lake cichlids). Water color is red-shifted at greater depths in these lakes, and male benthics raised in red-shifted water in the laboratory develop less red and more black coloration than those raised in clear water (Lewandowski and Boughman, 2008). It would be informative to know whether this response to ambient light is present in the marine stickleback (i.e., the presumed ancestor). If so, and if the sensitivity of females to red light is similarly affected, then reproductive isolation between the ecotypes might have arisen as a byproduct of plastic responses to the environment (process 8). Alternatively, or in addition, the ecotype differences in color and red sensitivity might have evolved in response to selection favoring increases in the visibility of males against the background water color (process 6).

Indigobirds

Research on brood-parasitic indigobirds (*Vidua* spp.) by Michael Sorenson, Robert Payne, and colleagues (2003) illustrates how within-generation shifts in the development of secondary sexual traits and mate preferences (process 8) could cause rapid speciation. Indigobird nestlings, which are invariably raised by foster parents, imprint on the songs of their host species. Males later attract females reared by the same host species by mimicking host songs (Fig. 2), and females preferentially lay eggs in the nests of their host species. Normally, this process of sexual imprinting maintains host-specificity between generations. But when females lay eggs in the nest of species other than their natal host, sexual imprinting may result in the sudden formation of new host races, or hybridization between existing host races, depending on whether the novel host already has its own host race of indigobirds (Sorenson et al., 2003). Molecular genetic data support this model of sympatric speciation with occasional hybridization. As a possible example of speciation in action, one of the 10 recognized parasitic indigobird species occurs in two morphologically indistinguishable host races. Males sing host-specific songs and respond more aggressively to songs of their own host race. Reproductive isolation between the host races is not complete, however, which indicates that colonization of new hosts alone may not be sufficient to cause speciation (Balakrishnan et al., 2009). Divergent selection caused by differences in host ecology (process 6) or selection against individuals of mixed-race parentage (process 2) may be required for complete reproductive isolation.

Darwin's finches

Peter and Rosemary Grant's long-term study of Darwin's finches has provided an even more compelling example of how sexual imprinting can result in almost instantaneous speciation (Grant and Grant 2024). A male immigrant with a distinctive song appeared on the island Daphne Major in 1981. Genomic analyses revealed the immigrant to be a hybrid between *Geospiza fortis*, which occurs on Daphne Major, and *G. conirostris*, which occurs on other islands. The immigrant mated with a female *G. fortis* and his offspring evidently imprinted on his distinctive song. By the third generation and up until at least the sixth generation, the new hybrid lineage was functioning as a new species, isolated from *G. fortis* only by male song and female song preferences, with no indications of diminished fitness (Fig. 3).

Other study systems that have provided valuable insights into the role of sexual selection in speciation include Hawaiian *Drosophila*, Pacific salmon (*Oncorhynchus*), and water striders

(Gerridae), among others. See review articles by Ritchie (2007), Mullen and Shaw (2014), Schaefer and Ruxton (2015), Tinghitella et al. (2018), Lindsay et al. (2019), and Mendelson and Safran (2021) for discussion of these and other examples. For a systematic review of case studies of male-male competition and speciation, see Lackey et al. (2024).

Experimental Evolution Studies

Laboratory evolution experiments have been used to test a wide range of hypothesized speciation mechanisms (Rice and Hostert 1993, White *et al.* 2020), some of which involve shifts in mate preferences or intrasexual competition (e.g., Villa et al. 2019). Here we focus narrowly on evolution experiments that were designed to test the hypothesis that sexual selection can ‘drive’ speciation. In this context, experimental evolution refers to the approach of establishing replicate laboratory populations or lines, maintaining them under specific treatments that are thought to represent different intensities of sexual selection (e.g., monogamy vs. polygamy), and testing for reproductive isolation between lines after multiple generations. This method has the potential to demonstrate the efficacy of particular scenarios for generating reproductive isolation. For example, an experimental evolution study with dungflies (*Sepsis cynipsea*) showed incipient reproductive isolation (assortative mating) after 35 generations under conditions promoting sexual conflict (Fig. 4).

Most evolution experiments designed to test the hypothesis that sexual selection drives speciation have not yielded any signs of reproductive isolation (reviewed by Plesnar-Bielak et al. 2013; White et al. 2020). One possible explanation for the negative results is that replicate populations exposed to the same selection regimes do not evolve in arbitrarily different directions. For example, male adaptations to overcome female resistance to mating and female counteradaptations may evolve in parallel, from a common starting point, as opposed to diverging between selection lines. If so, this would imply that sexual conflict alone is unlikely to cause speciation. But perhaps sexual conflict would cause divergence between populations that inhabit environments that differ in ways that affect the cost of female resistance or the efficacy of male mating tactics, etc. A potentially promising direction for future research would be to incorporate such environmental gradients into experimental evolution studies.

Adding genomic analyses to evolution experiments might lead to insights about how the genetic architecture of sexual traits affects the likelihood of sexual selection driving speciation. An evolution experiment on fruit flies (*Drosophila pseudoobscura*) seemed designed to do just that: sexual selection intensity was manipulated using monogamous and polyandrous lines and divergence was tracked at the level of SNP allele frequencies for ~160 generations (Wiberg et al, 2021). Divergence was found to be concentrated in regions of the genome that contain candidate genes for courtship and mating – exactly the sorts of genes that could be involved in reproductive isolation – but unfortunately, the level of incipient reproductive isolation between lines was not measured.

Conclusions

Research on speciation, at least in animals, needs to take sexual selection into account. On the other hand, the quest for examples of speciation driven purely by sexual selection may be misguided. Theoretical work shows that speciation is more likely when divergent sexual selection is coupled with ecological divergence, and empirical studies suggest that the situation in nature is even more complex. While it is generally productive in science to pit alternative

hypotheses against each other, in this case, the hypothesized processes may be integral parts of a more complex process. A goal for future modeling should be to evaluate which combinations of processes most readily yield speciation.

Few empirical studies of sexual selection and speciation are directly comparable, and each well-studied system has yielded unique insights. There are many well-documented examples of allopatric populations that have diverged in mate preferences or secondary sexual characters, but most such studies stop short of determining whether the populations are reproductively isolated and, if so, whether the observed phenotypic differences are responsible. The Hawaiian crickets illustrate the problem with assuming that reproductive isolation is caused by an observed difference in traits and preferences. Future case studies should go beyond identifying plausible mechanisms of prezygotic isolation to showing whether these mechanisms actually operate in nature.

Another promising direction for future research will be to use the experimental evolution approach to identify the conditions under which particular modes of sexual selection generate reproductive isolation. Evolution experiments that include environmental gradients, mating assays, and genomic analyses could help identify ecological and genomic factors that influence speciation in the wild and lead to refinements of theory.

Research on sexual selection in plants has advanced in recent years, but hypothesized mechanisms linking sexual selection to speciation in plants remain largely untested (reviewed by Haghghatnia *et al.* 2023). Plants exhibit a wider diversity of reproductive strategies than animals and thus may offer unique opportunities to study general principles that govern sexual selection and speciation.

Understanding how sexually selected traits contribute to speciation could have conservation applications. In one of the first studies to draw attention to the diversity-maintenance aspect of sexual selection, Ole Seehausen and colleagues (1997) provided compelling evidence that species-level diversity in African Lake cichlids has declined in part because species that formerly were reproductively isolated by color-based mate preferences have merged through hybridization because pollution from agricultural run-off made the water too turbid for color differences to be distinguished. More recently, Heidi Fisher and colleagues (2006) showed that chemosensory-based reproductive isolation between two swordtail (*Xiphophorus*) species was so severely disrupted by anthropogenic chemicals that nearly all of the fish in one polluted river were hybrids. These examples illustrate just two of the many ways that human activities inadvertently interfere with mate choice in wild animals resulting in population declines, hybridization, and extinction (reviewed by Boughman *et al.* 2024). Examples of successful conservation interventions are rarer, but identifying the causes of biodiversity loss is a crucial first step.

Acknowledgments

The senior author dedicates this article to his PhD advisor, William J. Hamilton III, who passed away in 2006.

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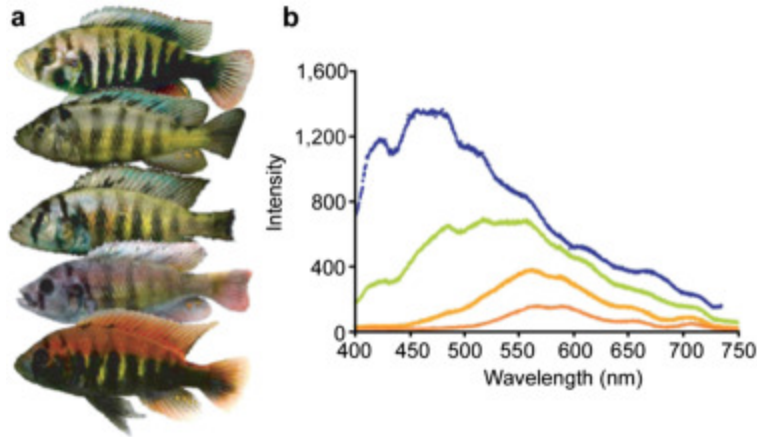


Fig. 1 (a) Variation in male nuptial coloration in sympatric *Pundamilia* spp. cichlids of Lake Victoria, from the blue form of typical *Pundamilia pundamilia* (top) to the red form of typical *Pundamilia nyererei* (bottom). Females of both species have cryptic yellowish coloration. The red species *P. nyererei* is found at greater depths than the blue species *P. pundamilia*. (b) An illustration of how the spectrum of ambient light changes with depth in Lake Victoria, from the surface (blue) through three successive depths: 0.5 m (green), 1.5 m (orange), and 2.5 m (red).

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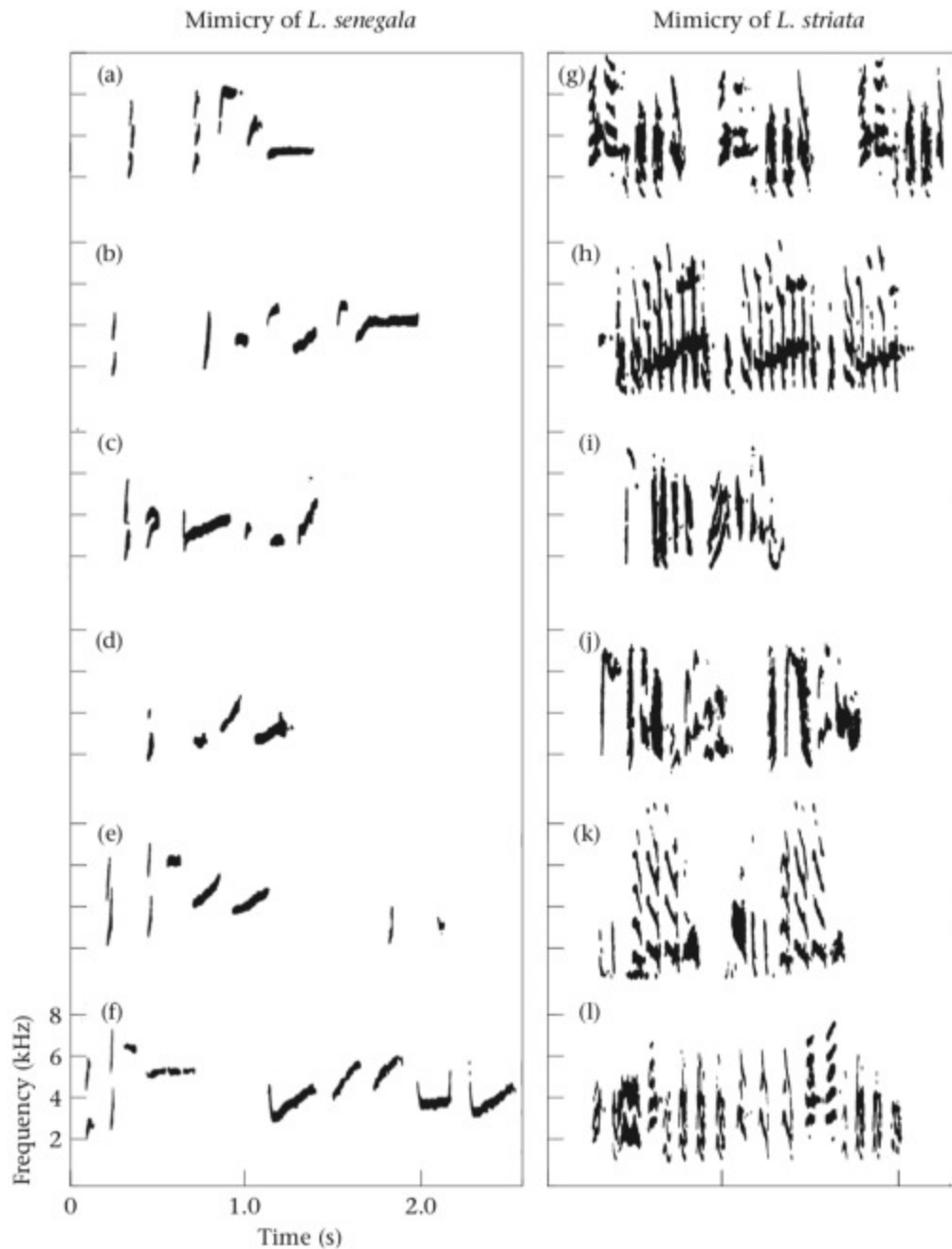


Fig. 2 Sonograms showing host mimicry by male indigobirds (*Vidua chalybeata*). Males represented in the left column were reared by the normal firefinch host, while those represented in the right column were reared by Bengalese finches.

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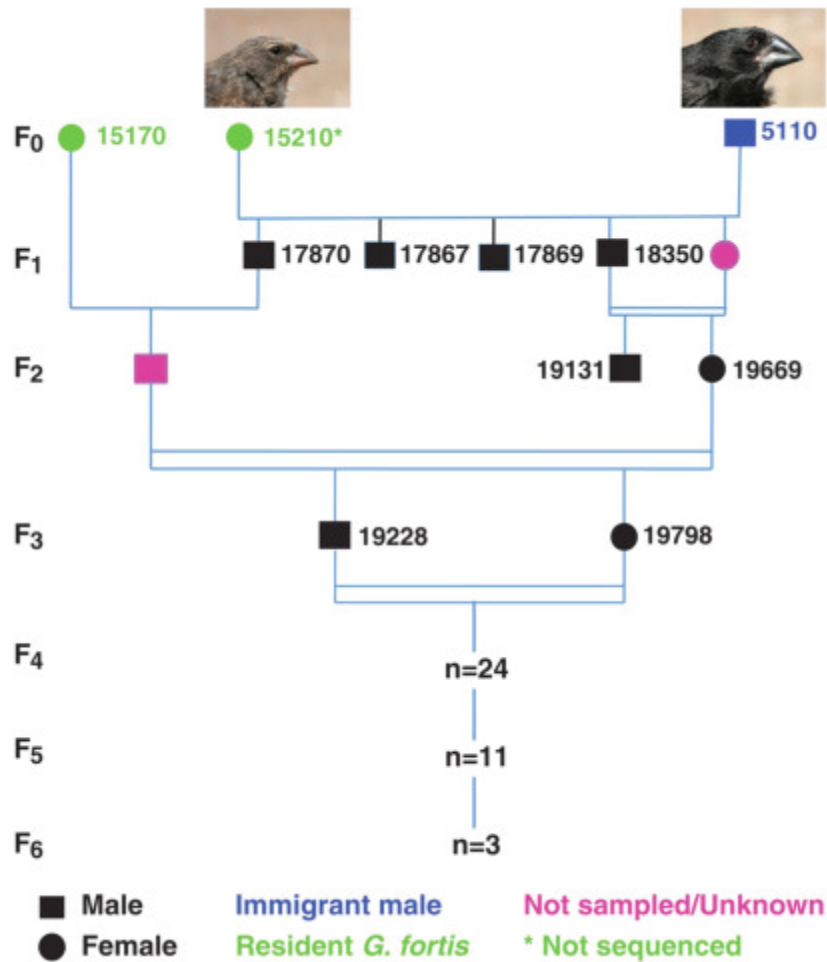


Fig. 3 The lineage of a new, incipient species of Darwin's finch on Daphne Major. The founding immigrant male is shown in the upper right. Lines connect parents and offspring. The numbers through generation F₃ identify individual birds. In generations F₄–F₆, the number of individuals is indicated by n. Note that after generation F₁, all matings are between descendants of the founding male.

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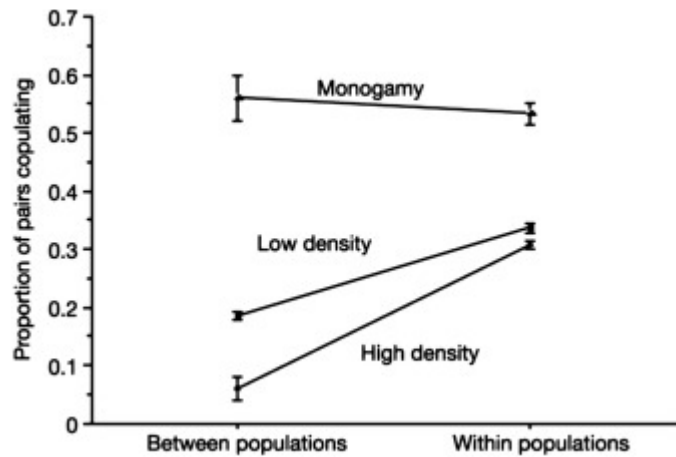


Fig. 4 Results of experimental evolution study on dungflies. The graph shows incipient reproductive isolation between populations (lines) of flies maintained under conditions conducive to sexual conflict (low-density and high-density treatments) but not between populations maintained under monogamy, after 35 generations. Error bars indicate ± 1 standard error.

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Table 1 Processes that could contribute to reproductive isolation by causing populations to diverge in secondary sexual characters and mate choice

Process	Definition in this context
1. Genetic drift	Shifts in secondary sexual characters or mate preferences caused by genetic bottlenecks or founder events
2. Reinforcement	Evolution of increased prezygotic reproductive isolation between sympatric populations in response to selection against hybrids
3. Fisherian selection	Co-evolution of male secondary sexual characters and female preferences arising from the genetic correlation between the sexes
4. Sexual conflict	Co-evolution of male secondary sexual characters and female resistance to mating
5. Intrasexual competition	Shifts in phenotypic traits or mating patterns caused by mate competition (e.g., contest competition, scramble competition, territoriality)
6. Local adaptation	Selection arising from shifts in the local optima of secondary sexual characters or mate preferences (e.g., sensory drive, predation)
7. Pleiotropy or linkage	Shifts in secondary sexual characters or mate preferences caused by selection on genetically correlated traits (e.g., body size)
8. Phenotypic plasticity	Within-generation shifts in the development or expression of secondary sexual characters or mate preferences (e.g., song learning, sexual imprinting)