Sexual Selection and Speciation ☆

GF Grether, University of California, Los Angeles, CA, United States

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. Recent 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

Historical Background

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. 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 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.

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. I, therefore, restrict my attention here to processes leading to prezygotic isolation (with or without postzygotic isolation).

☆ *Change History*: February 2016. GF Grether updated the text and added some new references. April 2018: GF Grether, updated the text, inserted citations, and added several new references and Figure 3.
This is an update of G.F. Grether, Sexual Selection and Speciation, Reference Module in Life Sciences, Elsevier, 2018.

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	Divergence in secondary sexual characters caused by agonistic interactions (e.g., 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
8. Phenotypic plasticity	Within-generation shifts in the development or expression of environmentally sensitive secondary sexual characters or mate preferences

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 and/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 would yield a correlated response in the other, and thus, geographic variation in the strength of survival selection could result in a pattern of correlated variation in secondary sexual traits and mate preferences. While theoreticians have tended to focus on speciation via sexual selection in the strict sense, 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 links that are most often explored by theoreticians 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). For a review of the possible ways that trait divergence caused by intrasexual competition could contribute to speciation, see Tinghitella *et al.* (2018) and commentaries by Simmons (2018) and McCullough and Emlen (2018).

In general, however, 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 strength of survival selection on the male 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 sexual selection is coupled with ecological (niche) divergence (e.g., van Doorn et al., 2009). Models based only on disruptive sexual selection yield sympatric speciation under more restrictive conditions than models that also allow ecological character displacement to occur (Ritchie, 2007).

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) concludes that Fisherian selection actually undermines the speciation process, under most circumstances.

Models by Sergey Gavrilets and colleagues (Gavrilets and Hayashi, 2005; Gavrilets, 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.

From an empirical standpoint, 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 have been put forth as evidence that sexual selection plays a role in speciation. Here, I 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 increases speciation rates or decreases extinction rates. There are several reasons to think that sexual selection might increase extinction rates, and fewer reasons to expect the reverse (but see M'Gonigle et al., 2012). Hence, these results have been taken as evidence that sexual selection increases speciation rates. One 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, complex song, or bright 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 in Ritchie, 2007).

In a phylogenetic analysis relating song to morphology across 163 species of antbirds (Thamnophilidae), Seddon (2005) tested predictions based on pleiotropy, local adaptation, and species recognition. 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 postspeciation reproductive character displacement. However, evolutionary age is a potentially confounding factor in such studies; sympatric lineages might differ more in sexual characters because they are older, on the average, than allopatric lineages. In a large comparative study of ovenbirds (Furnariidae), Tobias et al. (2014) found that all patterns of character divergence in sympatry disappeared after controlling for lineage age.

Case Studies

The East-African lake cichlids 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 morph-specific female preferences, and may be in the process 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 Seehausen and Schluter (2004) is that intrasexual (male–male) competition over breeding territories favors rare color morphs (process 5), 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 towards 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) have proposed a complex verbal model of the speciation process that includes sensory drive, Fisherian selection, gene flow, and reinforcement.

Hawaiian crickets in the 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. Mendelson and Shaw (2005) found that female *Laupala* can discriminate between conspecific and heterospecific song from a distance and are more likely to 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 F_2 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).

Three-spine sticklebacks provide an example in which sexual selection and ecological character displacement both appear to have played integral roles in speciation. In the lakes of British Columbia, Canada, sticklebacks 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 have shown that male coloration and female sensitivity to red light differ between ecotypes in the same direction in three different lakes (Boughman et al., 2005). Compared to benthics, limnetic males have more red
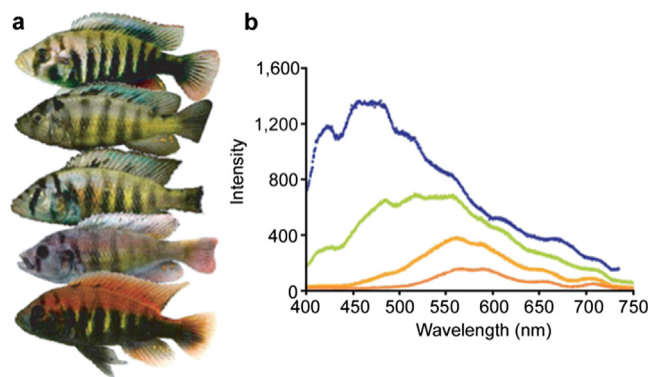

Fig. 1   (a) Variation in male nuptial coloration in sympatric *Pundamilia* spp. cichlids of Lake Victoria, from the blue form of typical *Pundamilia pundamilia* (top) to the red form of typical *Pundamilia nyererei* (bottom). Females of both species have cryptic yellowish coloration. The red species *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). Modified and reprinted by permission from Seehausen, O., Terai, Y., Magalhaes, I.S., et al., 2008. Speciation through sensory drive in cichlid fish. Nature 455, 620–626, with permission from Nature Publishing Group. Copyright Macmillan Publishers Ltd.

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). Reinforcement seems unlikely in this case because ecotypes differ only in the strength and not in the direction of the female color preference.

Research on brood-parasitic indigobirds (*Vidua* spp.) by Michael Sorenson, Robert Payne, and colleagues illustrates how within-generation shifts in the development of secondary sexual traits and mate preferences could cause rapid speciation (process 8). 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
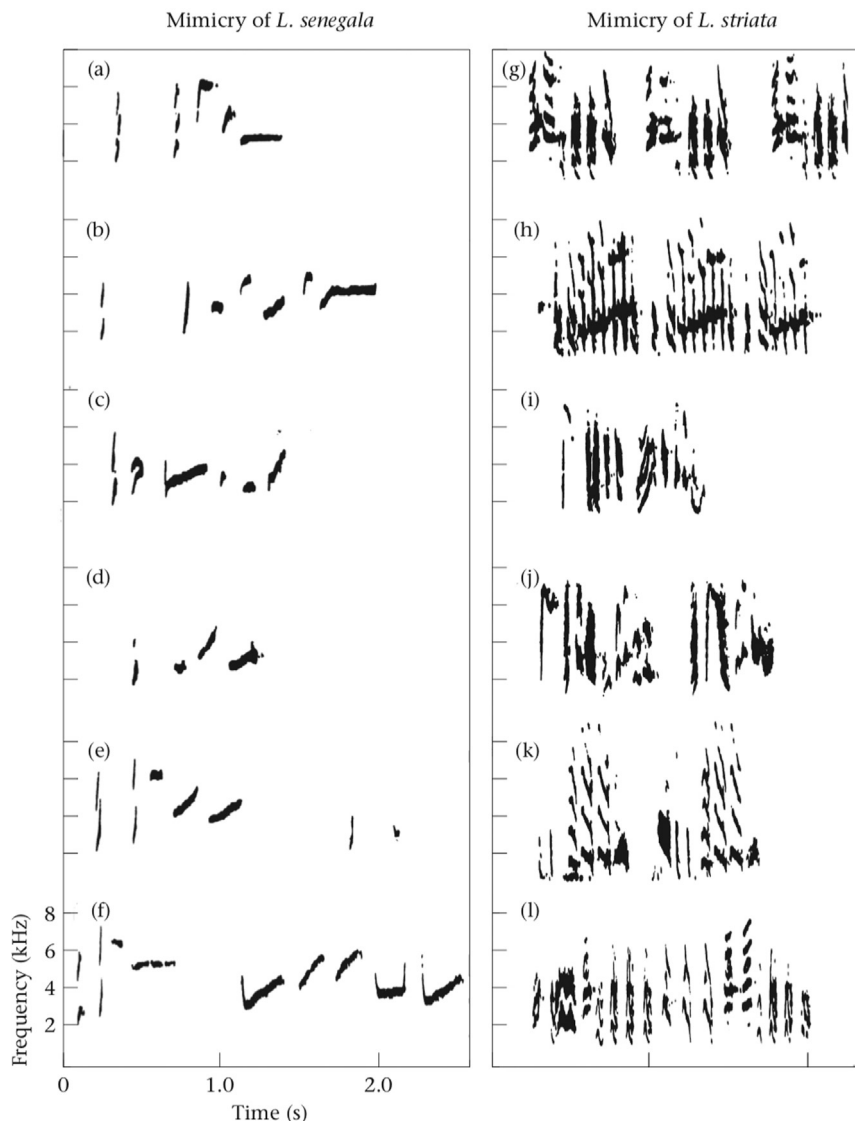

Fig. 2 Sonograms showing host mimicry by male indigobirds (*Vidua chalybeata*). Males represented in the left column were reared by the normal firefinch host, while those represented in the right column were reared by Bengalese finches. Reprinted with permission from Payne, R.B., Payne, L.L., Woods, J.L., Sorenson, M.D., 2000. Imprinting and the origin of parasite–host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. Animal Behavior 59, 69–81, with permission from Elsevier. Copyright Elsevier.
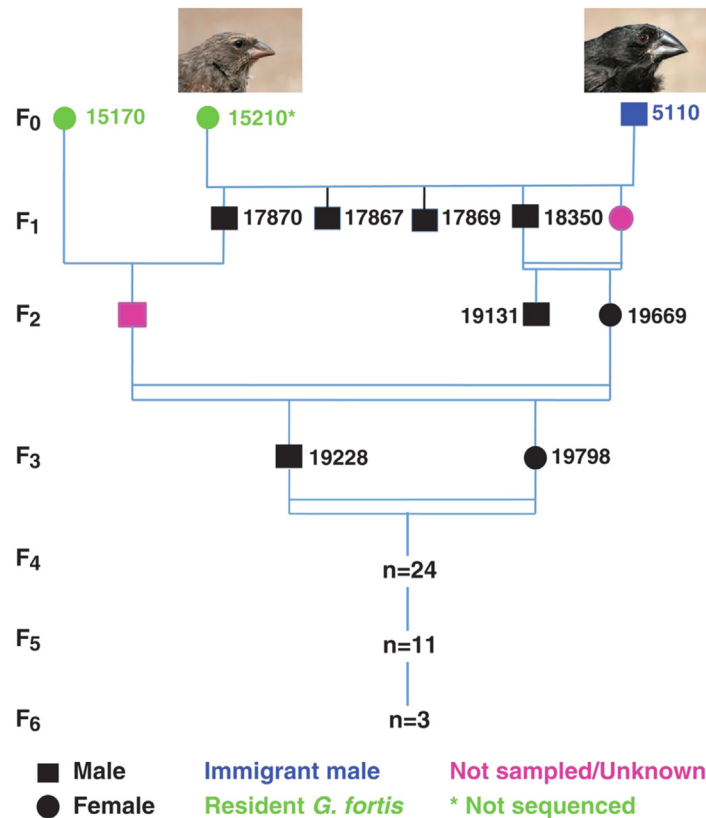
Fig. 3 The lineage of a new, incipient species of Darwin's finch on Daphne Major. The founding immigrant male is shown in the upper right. Lines connect parents and offspring. The numbers through generation F_3 identify individual birds. In generations F_4–F_6, the number of individuals is indicated by n. Note that after generation F_1, all matings are between descendants of the founding male. Reprinted by permission from Lamichhaney, F. Han, M.T., Webster, L., et al., 2018. Rapid hybrid speciation in Darwin's finches. Science 359, 224–228, with permission from AAAS.

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 ten 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) and/or selection against individuals of mixed race parentage (process 2) may be required for complete reproductive isolation.

Darwin's finches have provided an even more compelling example of how sexual imprinting can result in almost instantaneous speciation (process 8). A male immigrant with a distinctive song appeared on the Galapagos island of Daphne Major in 1981 and entered Peter and Rosemary Grant's long-term study (Grant and Grant, 2014). Genetic 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 hybrid mated with a female *G. fortis* and his offspring apparently imprinted on his distinctive song. Since the second generation, this new lineage has functioned as a new species, isolated from *G. fortis* only by male song and female song preferences, and is now in its 6th generation (Fig. 3; Lamichhaney et al., 2018).

Other study systems that have provided valuable insights into the role of sexual selection in speciation include Hawaiian *Drosophila*, Pacific salmon (*Oncorhynchus*), greenish warblers (*Phylloscopus*), and water striders (Gerridae), among others. See the review articles by Ritchie (2007), Mullen and Shaw (2014), and Schaefer and Ruxton (2015) for discussion of these and other examples.

Experimental Evolution Studies

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. An experimental evolution study with dungflies showed
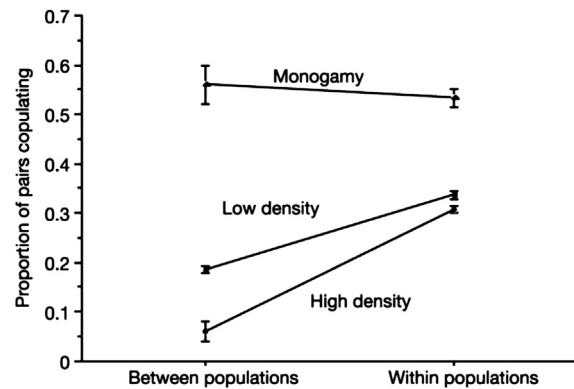
Fig. 4   Results of experimental evolution study on dungflies. The graph shows incipient reproductive isolation between populations (lines) of flies maintained under conditions conducive to sexual conflict (low-density and high-density treatments) but not between populations maintained under monogamy, after 35 generations. Error bars indicate ±1 standard error. Reprinted by permission from Martin, O.Y., Hosken, D.J., 2003. The evolution of reproductive isolation through sexual conflict. Nature 423, 979–982, with permission from Nature Publishing Group. Copyright Macmillan Publishers Ltd.

incipient reproductive isolation (assortative mating) after 35 generations under conditions promoting sexual conflict (Fig. 4), but similar experiments on several other species of insects have failed to yield any signs of reproductive isolation (e.g., Bacigalupe et al., 2007)

One possible explanation for the negative results is that replicate populations exposed to the same selection regimes do not evolve in arbitrarily different directions; that is, adaptations to overcome female resistance 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. One promising direction for future research would be to incorporate such environmental gradients into experimental evolution studies.

Conclusions and Future Directions

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.

Behavioral ecologists have recently begun to pay more attention to species in which females develop secondary sexual characters. It is not clear yet whether female-specific secondary characters are products of sexual selection or some other form of social selection (e.g., resource competition). The role of female secondary sexual characters and male mate choice in speciation is a wide open question.

Acknowledgments

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