



Sexual Selection and Speciation

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Introduction

The widespread observation that for many closely related taxa, sexual traits differ more markedly than other traits, underpins the hypothesis that sexual selection is often a major cause of speciation. Quite a few empirical studies support this hypothesis, by demonstrating that the traits that are targets of sexual selection within species are also critical to premating reproductive isolation (sexual isolation) between species. Despite these convincing studies, the hypothesis remains controversial. Fueling the controversy, results from comparative analyses are equivocal, with some studies providing support, others failing to find any relationship between sexual selection and speciation metrics, and others actually suggesting that sexual selection is more likely to cause extinction than speciation. Theoretical work is likewise mixed. Because of these mixed results, we lack a general answer to this question: Does sexual selection cause speciation?

General Overviews of Speciation

Several books have done an excellent job in reviewing the recent progress and potential for future studies in speciation. Those works included in this section touch on the role of sexual selection, but no book yet addresses it as a primary focus. Coyne and Orr 2004 is the most general. Schluter 2000, which focuses on adaptive radiation and the role of ecology and selection, has influenced the burgeoning field of ecological speciation, which Nosil 2012 reviews. Although Price 2008 focuses on birds, the book also raises many generalities of importance to other taxa. Gavrillets 2004 presents a novel and influential theoretical framework that has brought heightened attention to using fitness landscapes to understand diversification.

Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sunderland, MA: Sinauer.

This book should be considered “canon” for anyone studying speciation. It reviews speciation through many mechanisms (not just sexual selection), and provides evidence across a wide array of taxa for the generalities of the speciation process. It is extremely valuable in consolidating and making clear the patterns and patches of knowledge in speciation research, and serves as an excellent guide, particularly for those beginning to study speciation.

Gavrillets, S. 2004. *Fitness landscapes and the origin of species*. Princeton, NJ: Princeton Univ. Press.

Gavrillets’s book provides important theoretical insight and synthesizes mathematical models of speciation, including those that explore sympatric speciation and sexual selection. Gavrillets develops a novel analytical approach to the highly dimensional nature of selection. His “holey landscape” framework recognizes that many genotypic and phenotypic combinations will have high fitness, flattening the fitness landscape and facilitating evolution. However, some combinations have low fitness, falling into fitness “holes.”

Nosil, P. 2012. *Ecological speciation*. Oxford: Oxford Univ. Press.

This book nicely reviews the available evidence on the ecological processes that form new species, and tackles several controversial topics. The focus is on natural selection, but there is some treatment of how assortative mating can evolve through sexual selection as well.

Through examining findings from manipulative experiments, genomics, and theoretical literature on ecological speciation, this book synthesizes our current understanding and offers predictions for future research directions. Particularly useful are ideas for better integration of empirical and theoretical work.

Price, T. D. 2008. *Speciation in birds*. Greenwood Village, CO: Roberts.

Price's approach is refreshing, as it advocates for integrating ecology, behavior, and genetics in understanding speciation. Although this book deals only with birds, its synthesis and insights are important for understanding general patterns of speciation, and the role for sexual and natural selection. Price embraces the social selection perspective of M. J. West-Eberhard (see West-Eberhard 1983, cited in the Early History of Sexual Selection and Speciation), and discusses how song learning affects the evolution of premating isolation.

Schluter, D. 2000. *The ecology of adaptive radiation*. Oxford: Oxford Univ. Press.

This book focuses on the ecological causes of diversification due to divergent natural selection among environments, and also considers situations in which sexual selection depends on environment (such as sensory drive). It systematically considers the causes of adaptive radiation due to ecological differences and provides many detailed natural examples, pointing out challenges, the state of current evidence, and unexplored theoretical territory. Its lucid presentation makes this an excellent entry to speciation research.

The Early History of Sexual Selection and Speciation

Charles Darwin first understood the importance of sexual selection for evolutionary change and diversification, dedicating the majority of an entire book to the subject (Darwin 1871). However, sexual selection was largely forgotten, especially Darwin's (at the time) controversial view that female choice could be a selective force. An important exception is Fisher 1930, which dedicates an entire chapter to sexual selection, including how it could affect speciation. The author's verbal models came to form the basis of both runaway and good genes models of sexual selection. However, sexual selection research remained rather dormant until the 1980s. Lande 1981 was crucial in renewing interest in the topic of sexual selection generally and its role in speciation more specifically with its mathematical description of Fisher's runaway process. Lande saw that rapid coevolution between preference and display trait could lead to speciation when preferences change arbitrarily between populations. The subsequent West-Eberhard 1983 is an influential review of how "social selection," including sexual selection, could impact speciation. Lande and Kirkpatrick are responsible for many influential mathematical models studying sexual selection; their paper Lande and Kirkpatrick 1988 suggests that sexual selection linked to ecologically important traits would quicken speciation, and Lande 1981 has been extremely influential and is the starting point for many modeling papers on sexual selection in general and speciation via sexual selection in particular. Andersson 1994 summarizes sexual selection research up to the book's publication, dedicating a chapter to how sexual selection could impact "species recognition traits." The renewed interest in sexual selection and the recognition that it could create reproductive barriers between populations has caused a flurry of research on the topic, beginning with comparative studies (see Testing Generalities with Comparative Analysis).

Andersson, M. B. 1994. *Sexual selection*. Princeton, NJ: Princeton Univ. Press.

Although this book was published in the late 20th century, it is still the best place to start for a broad overview of sexual selection with many different empirical examples. Andersson dedicates an entire chapter to speciation, focusing primarily on how sexual selection influences speciation recognition traits.

Darwin, Charles. 1871. *The descent of man, and selection in relation to sex*. London: Murray.

Darwin dedicated the majority of this book to describing his ideas regarding sexual selection. In addition to distinguishing male competition and female choice as critical selective forces, this book is full of interesting natural history examples of ornaments and weapons.

Fisher, R. A. 1930. *The genetical theory of natural selection*. Oxford: Clarendon.

Fisher's work represents a resurgence of the importance of sexual selection as a subset of natural selection driving the evolution of species. Readers should focus on his verbal models of sexual selection, which have ultimately become the basis of runaway and good genes models of sexual selection, and which make an important contribution to our understanding of how sexual selection and speciation may interact.

Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America* 78:3721–3725.

This paper lays out the theoretical basis for speciation by sexual selection and is still used in models. Specifically, it explores the joint evolution of mating preferences and display traits, which can result in a runaway coevolutionary process resulting in extreme elaboration of male traits. The paper's parameters, particularly the initial conditions and sources of selection in the model, have been subsequently tweaked and tested to discover conditions under which speciation due to this process does and does not occur.

Lande, R., and M. Kirkpatrick. 1988. Ecological speciation by sexual selection. *Journal of Theoretical Biology* 133:85–98.

This theory paper establishes through quantitative genetic models that female mate choice based on ecologically important male characters can drive speciation. The paper elegantly proposes that, when more than one ecological niche is available, mate preference for genetically inherited traits for local adaptation can push populations out of deep adaptive valleys into reproductively isolated populations through both pre- and post-mating mechanisms. The theory presented provides an important link between sexual and natural selection in promoting speciation, even in sympatry.

West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Reviews in Biology* 58:155–183.

One of the classic papers on sexual selection. The author recognizes that social interactions can generate selection on the interacting partners, and this selection can be quite strong and dynamic. Sexual selection is one such form of social selection. The logic of these ideas is described, many examples are given, and the connection to speciation is made.

Testing Generalities with Comparative Analysis

If sexual selection increases the likelihood of population divergence in traits important for reproductive success, speciation rates should be associated with the strength or divergence of sexual selection. Darwin himself suggested that genera with more elaborate sexual traits seemed more species rich (Darwin 1871, cited in the *Early History of Sexual Selection and Speciation*). This prediction has more recently been systematically tested by using comparative methods, although primarily in birds because of the wealth of detailed information on both their biology and potentially sexually selected morphological traits. However, the results of these studies have been incredibly mixed; for every study demonstrating an effect of sexual selection (Owens, et al. 1999; Arnqvist, et al. 2000 [cited in the "Sexual Conflict and Speciation"]; Seddon, et al. 2013) there is one demonstrating no effect (Gage, et al. 2002; Morrow, et al. 2003; Huang and Rabosky 2014), sometimes even using similar datasets. An early review of this literature and important call to arms is Panhuis, et al. 2001. Kraaijeveld, et al. 2011 (cited in the *Major Controversy: Can Sexual Selection Cause Speciation on its Own?: Reviews*) gives a more recent and very extensive review of the comparative literature, finding overall support for sexual selection increasing speciation rates, although the effect size was very small. In particular, the authors propose methodological reasons for the disparity in the results of comparative analyses, such as phylogenetic depth and method of quantifying sexual selection. Rodríguez, et al. 2013 (cited in the *Mechanisms That Cause Female Preferences and Male Traits to Diverge: Other Mechanisms*) suggests the disparity in comparative studies may be due to an incorrect focus on the strength of sexual selection, when the real factor selecting for increased display divergence is the degree of divergence in mating preferences.

Gage, M. J. G., G. A. Parker, S. Nylín, and C. Wiklund. 2002. Sexual selection and speciation in mammals, butterflies and spiders. *Proceedings of the Royal Society of London B: Biological Sciences* 269:2309–2316.

One of the studies that focuses on non-avian taxa; Gage, and colleagues are interested in the effect that sexual conflict (differences between male and female optima in mating frequency and choice) has on speciation. The authors find no evidence for associations between polyandry or sexual size dimorphism and species richness in mammals, butterflies, or spiders.

Huang, H., and D. L. Rabosky. 2014. Sexual selection and diversification: Reexamining the correlation between dichromatism and speciation rate in birds. *American Naturalist* 184:E101–E114.

These authors use sophisticated comparative methods on a proxy for strength of sexual selection, plumage dichromatism, and speciation rates using a dataset of that is larger than that which the authors of Seddon, et al. 2013 used. Huang and Robosky find no relationship between dichromatism and speciation rate, even when taking a species-pair approach, despite finding large amounts of heterogeneity in speciation rates in the avian phylogeny.

Morrow, E. H., T. Pitcher, and G. Arnqvist. 2003. No evidence that sexual selection is an “engine of speciation” in birds. *Ecology Letters* 6:228–234.

This study uses the same phylogenetically independent contrast method as Gage, et al. 2002, but on a large avian dataset. The authors also find no evidence for associations between species richness and sexual dimorphism, sexual dichromatism, or testes size. They close by stating the hypothesis that sexual selection might increase the evolution of reproductive isolation between species, but it might also increase extinction rates, leading to no net effect on species richness.

Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: Body size, life history, sexual selection or ecology? *Proceedings of the Royal Society of London B: Biological Sciences* 266:933–939.

Although preceded by several other comparative studies on this topic, this paper stands out because of the authors' use of a much broader taxonomic dataset (although still only birds) and testing of additional hypotheses explaining variation in species richness. They use sister-pairs of families and find that species richness is predicted by sexual dichromatism, not body size or life history, although ecological generalism and dispersal ability are also important predictors.

Panhuis, T. M., R. Butlin, M. Zuk, and T. Tregenza. 2001. Sexual selection and speciation. *Trends in Ecology and Evolution* 16:364–371.

Actually part of an entire issue on speciation, this paper is an important critique of the evidence for sexual selection and speciation, with a focus on comparative studies, but also reviewing the little empirical data available at that time. The authors conclude with an influential set of criteria for demonstrating that sexual selection has a positive impact on speciation.

Seddon, N., C. A. B. Botero, P. O. Dunn, et al. 2013. Sexual selection accelerates the evolution of phenotypic divergence and reproductive isolation in birds. *Proceedings of the Royal Society of London B: Biological Sciences* 280:20131065.

This study uses a sister-taxa approach in birds to focus on recent speciation events (tips of the phylogeny) and focus on whether phenotypic divergence is related to sexual dichromatism. The authors' statistical analyses are more sophisticated than previous sister-taxa studies. They find moderate support for the hypothesis that sexual selection increases phenotypic divergence in traits likely to be important for reproductive success.

Testing Generalities with Other Approaches

In addition to using comparative approaches to explore general patterns, researchers use other approaches to test the general mechanisms that underlie the process of speciation by sexual selection. Important to this effort are theoretical approaches exploring the nature of selection for increased assortative mating (Bolnick and Doebeli 2003; Cooper, et al. 2011; Otto, et al. 2008; Servedio and Bürger 2014). An early review (Turelli, et al. 2001) in the special Speciation issue of *Trends in Ecology & Evolution* covered older theory than some of the other papers included here. Another general topic dealt with in the opinion piece Mendelson and Shaw 2012 is whether species recognition and mate recognition are distinct or similar mechanisms. Also included in this section is a paper focused on how best to estimate sexual isolation (Rolán-Alvarez and Caballero 2000), important for anyone actually trying to do so.

Bolnick, D. I., and M. Doebeli. 2003. Sexual dimorphism and adaptive speciation: Two sides of the same ecological coin. *Evolution* 57:2433–2449.

This theory paper shows that intraspecific competition can give rise to sexual dimorphism or adaptive speciation, but seldom both, depending on the genetic independence of traits and strength of assortative mating. It is the first to show speciation from negative assortative mating, and connects ecological conditions to evolutionary diversity. It is also an excellent example of combining different speciation modeling techniques within the same paper.

Cooper, I. A., R. T. Gilman, and J. W. Boughman. 2011. Sexual dimorphism and speciation on two ecological coins: Patterns from nature and theoretical predictions. *Evolution* 65:2553–2571.

This paper combines data on dimorphism and assortative mating from stickleback fish with theory, recognizing that trade-offs caused by partitioning a single ecological resource may be overcome by partitioning multiple ecological axes. When those axes are even partly independent, dimorphism and speciation can both evolve. Dimorphism evolves quickly and often, whereas speciation is rare and takes time, explaining why many natural examples show the evolution of both dimorphism and speciation.

Mendelson, T. C., and K. L. Shaw. 2012. The (mis)concept of species recognition. *Trends in Ecology and Evolution* 27:421–427.

This controversial review claims that those studying mate choice and mate recognition have confused the issue by dichotomizing these processes. It is not clear that this is really the case; however, this opinion paper is valuable in drawing attention to an important research question: are the same proximate and/or ultimate mechanisms involved when individuals make mate-choice decisions within versus between species?

Otto, S. P., M. R. Servedio, and S. L. Nuismer. 2008. Frequency-dependent selection and the evolution of assortative mating. *Genetics* 179:2091–2112.

This model provides a link between frequency-dependent fitness and assortative mating in sympatry, showing indirect selection for assortative mating through lower fitness of heterozygotes even with moderate costs to assortative mating. Critically, this paper shows that the model conditions to generate assortative mating may differ from those that maintain it, and also provides an excellent overview of prior models and their conditions that future theory papers would be wise to emulate.

Rolán-Alvarez, E., and A. Caballero. 2000. Estimating sexual selection and sexual isolation effects from mating frequencies. *Evolution* 54:30–36.

This paper describes a standardized method for estimating sexual isolation from empirical data; this method allows for comparison among systems.

Servedio, M. R., and R. Bürger. 2014. The counterintuitive role of sexual selection in species maintenance and speciation. *Proceedings of the National Academy of Sciences of the United States of America* 111:8113–8118.

Lande 1981, a formalization of Fisher's runaway model reported in Fisher 1930 (both cited in the Early History of Sexual Selection and Speciation), is the typical starting point for theoretical research on sexual selection and speciation. However, this landmark theoretical paper shows instead that Fisherian sexual selection often inhibits speciation. This finding is especially likely in secondary contact when sexually selected traits are also under ecologically divergent selection. Therefore, forms of sexual selection other than Fisherian runaway may be necessary to foster diversification.

Turelli, M., N. H. Barton, and J. A. Coyne. 2001. Theory and speciation. *Trends in Ecology and Evolution* 16:330–343.

This review compares, contrasts, and supports with empirical data some verbal and mathematical theories of speciation by multiple mechanisms. The authors consider limitations of mathematical models and advocate for generating empirical data and verbal theory over mathematical theory because of the complexities involved in the speciation process. The authors treat very nicely the theoretical work on speciation by sexual selection.

Major Controversy: Can Sexual Selection Cause Speciation on its Own?

Along with the controversy about generality is another: Does speciation by sexual selection require synergistic natural selection, or can sexual selection cause speciation on its own? Often traits that isolate species are under both natural and sexual selection. Proponents of ecological speciation therefore argue that the primary cause of differentiation in these traits (and their role in speciation) is natural selection and, moreover, that divergence in female mating preferences is much more likely to arise via natural than sexual selection (Hine, et al. 2011 [cited in Empirical and Theoretical Tests]). However, many studies show convincingly that sexual selection is stronger than natural selection and therefore causes more rapid evolutionary change, and that it is pivotal to the evolution of reproductive isolation (Boul, et al. 2007; Mendelson 2003; and M'Gonigle, et al. 2012 [cited in Empirical and Theoretical Tests]; and Svensson, et al. 2006 [cited in Major Controversy: Can Sexual Selection Cause Speciation on its Own?: Reviews]). Still others suggest it is by their interaction that speciation is facilitated (Blows 2002 and van Doorn, et al. 2009 [cited in Empirical and Theoretical Tests]; and Kraaijeveld, et al. 2011; Maan and Seehausen 2011; Ritchie 2007 [all cited in Major Controversy: Can Sexual Selection Cause Speciation on its Own?: Reviews]).

Empirical and Theoretical Tests

Various empirical approaches have been used to explore this question, including experimental evolution (Blows 2002, Hine, et al. 2011), phylogenetic comparative analysis (Wagner, et al. 2012), manipulative experiments (Boul, et al. 2007; Mendelson 2003; Podos 2001), and theory (M'Gonigle, et al. 2012; van Doorn, et al. 2009).

Blows, M. W. 2002. Interaction between natural and sexual selection during the evolution of mate recognition. *Proceedings of the Royal Society of London B: Biological Sciences* 269:1113–1118.

A powerful way to address this controversy is through experimental evolution. This innovative study uses sexual and natural selection alone and in combination. Having natural selection alone reveals the cost of male mating traits, sexual selection alone reveals the strength of female preference, and, importantly, this approach shows that divergence in mate recognition systems was greatest with both sexual and natural selection acting.

Boul, K. E., W. C. Funk, C. R. Darst, D. C. Cannatella, and M. J. Ryan. 2007. Sexual selection drives speciation in an Amazonian frog. *Proceedings of the Royal Society of London B: Biological Sciences* 274:399–406.

This paper makes a strong case that sexual selection is the primary cause of speciation in a neotropical frog. The authors combine data suggesting that sexual selection has caused divergence in male mating signals and female preferences for those signals, with data showing genetic differentiation is greater for taxa with diverged sexual traits while controlling for geographic distance.

Hine, E., K. McGuigan, and M. W. Blows. 2011. Natural selection stops the evolution of male attractiveness. *Proceedings of the National Academy of Sciences of the United States of America* 108:3659–3664.

Using experimental evolution, the authors find that divergence in male traits and the evolution of male attractiveness via sexual selection is strongly opposed by natural selection, which prevents further elaboration. The paper provides important data relevant to theories of sexual selection, and to divergence in mating traits.

Mendelson, T. C. 2003. Sexual isolation evolves faster than hybrid inviability in a diverse and sexually dimorphic genus of fish (Percidae: *Etheostoma*). *Evolution* 57:317–327.

This paper addresses controversies about the prominence of premating and postmating isolation in speciation, while at the same time testing that sexual selection is a likely cause of enhanced premating isolation. In doing so, it establishes the key role that sexual selection and sexual isolation played in the speciation of a diverse group of fish. The author shows that sexual isolation evolves well before hybrid inviability, demonstrating that speciation was not initiated by postmating isolation.

M’Gonigle, L. K., R. Mazzucco, S. P. Otto, and U. Dieckmann. 2012. Sexual selection enables long-term coexistence despite ecological equivalence. *Nature* 484:506–509.

In addition to providing visually appealing, easy-to-understand figures, this theory paper shows that the combined effects of spatial variation in carrying capacity and mate search costs allow for sexual preferences alone to maintain ecologically equivalent species. This novel explanation for species diversity is important because, unlike many prior models, it does not require ecological differentiation for species maintenance (although the model does not explain the start of speciation itself).

Podos, J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin’s finches. *Nature* 409:185–188.

This paper presents compelling evidence in Darwin’s finches that divergent natural selection on beak morphology for eating different foods results in correlated changes in song production. Song is under sexual selection for mate choice, and is also a key trait that prevents hybridization between species; thus, the study links divergent natural and sexual selection to reproductive isolation. It is an important paper because it is one of the first to make this connection.

van Doorn, G. S., P. Edelaar, and F. J. Weissing. 2009. On the origin of species by natural and sexual selection. *Science* 326:1704–1707.

Through a theoretical model, the authors show that disruptive ecological selection can drive the evolution of sexual preferences for traits that signal local adaptation. Importantly, this model integrates natural and sexual selection in achieving reproductive isolation, even in sympatry with substantial gene flow. In contrast to other models, divergent mating preferences are not required for speciation under this model; rather, gene flow between species is suppressed as a result of genotype-by-environment interactions on condition-dependent traits that determine mate attractiveness.

Wagner, C. E., L. J. Harmon, and O. Seehausen. 2012. Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* 487:366–369.

By combining information on lake ecology and sexually selected traits for African cichlids, the authors investigate the factors that underlie extensive adaptive radiation in some clades and its absence in others. They show that adaptive radiation depends on a combination of ecological opportunity, as evidenced by lake depth and solar gain, and strong sexual selection, as evidenced by dichromatism. This paper provides key evidence for factors that contributed to the explosive speciation of cichlids.

Reviews

There are a number of reviews and meta-analyses addressing this controversial topic. Maan and Seehausen 2011, and Strelman and Danley 2003 review empirical work and consider the interaction of sexual and natural selection. Weissing, et al. 2011 reviews theoretical work and, because of the difficulties that gene flow presents, focuses mostly on sympatric speciation. Kirkpatrick and Ravigné 2002 and Ritchie 2007 do an excellent job reviewing both empirical and theoretical work. Meta-analyses are used in Kraaijeveld, et al. 2011 and Svensson, et al. 2006 to test important hypotheses. By taking an overarching perspective, one can evaluate how commonly sexual selection acts alone or in concert with natural selection.

Kirkpatrick, M., and V. Ravigné. 2002. Speciation by natural and sexual selection: Models and experiments. *American Naturalist* 159:S22–S35.

For an excellent overview of models and empirical results, this paper lays out two very informative tables. The structure of the paper nicely categorizes speciation by several characteristics (form of selection, isolating mechanism, direct/indirect selection, one/two-allele system, and high/low initial divergence) for comparison and use when one is examining experimental results. Notably, it views geography (i.e., allo-, para-, or sympatry) through the lens of assortative mating, and makes generalizations about how and when speciation is likely to occur.

Kraaijeveld, K., F. J. L. Kraaijeveld-Smit, and M. E. Maan. 2011. Sexual selection and speciation: The comparative evidence revisited. *Biological Reviews* 86:367–377.

A meta-analysis and review of comparative tests of sexual selection and speciation. This paper is important because it finds a consistent small effect of sexual selection on speciation that wanes as time passes, possibly because species persistence requires ecological differentiation. Thus, both natural and sexual selection seem required for speciation. The authors also argue for using mate selectivity rather than trait elaboration or dimorphism as metrics.

Maan, M. E., and O. Seehausen. 2011. Ecology, sexual selection, and speciation. *Ecology Letters* 14:591–602.

This review evaluates the ways in which sexual and natural selection interact in causing diversification. The review of theory suggests that sexual selection is especially likely to contribute to speciation when it interacts positively with natural selection, but the authors note that empirical evidence to test the interaction between natural and sexual selection is quite limited.

Ritchie, M. G. 2007. Sexual selection and speciation. *Annual Review of Ecology, Evolution, and Systematics* 38:79–102.

This paper is valuable for its thorough review of theoretical results, and comparative and empirical evidence, considered primarily through a “geographic lens.” The author begins by noting that sexual isolation is likely the most important form of reproductive isolation in animals, and concludes that sexual selection is most effective in causing isolation in conjunction with natural selection.

Strelman, J. T., and P. D. Danley. 2003. The stages of vertebrate evolutionary radiation. *Trends in Ecology and Evolution* 18:126–131.

The authors propose that vertebrate adaptive radiations occur in stages, illustrated with several empirical examples. They suggest that taxa first diverge to exploit different habitats, then in trophic morphology, and finally in sexually selected traits. The paper hypothesizes that large radiations are characterized by the presence of sexual selection, and the hypothesized late action of sexual selection is opposite from the early action hypothesized in Kraaijeveld, et al. 2011.

Svensson, E. I., F. Eroukmanoff, and M. Friberg. 2006. Effects of natural and sexual selection on adaptive population divergence and premating isolation in a damselfly. *Evolution* 60:1242–1253.

One way to resolve the controversy over the importance of sexual and natural selection to speciation is to directly compare the strength of both kinds of selection in natural populations. This paper does that, as well as characterizes the fitness landscapes for both. Sexual

selection is both stronger and more divergent than natural selection. Whereas sexual selection leads to moderate premating isolation, natural selection does not, suggesting that sexual selection plays a stronger role in population divergence.

Weissing, F. J., P. Edelaar, and G. S. van Doorn. 2011. Adaptive speciation theory: A conceptual review. *Behavioral Ecology and Sociobiology* 65:461–480.

This review addresses the conditions under which speciation can be driven by selection, comparing both strengths and weaknesses of models with ecological and/or sexual selection, and developing a new integrated, complementary model. The authors conclude that mating must reflect ecological characteristics for speciation to occur, although mating preferences need not diverge. Figure 1 is particularly useful in visualizing how sexual and natural selection speciation models have been treated separately, but clearly overlap conceptually.

Magic Traits

An idea that has gotten a lot of attention is that speciation can be greatly facilitated when sexual isolation is caused by divergent adaptive traits that also cause assortative mating. These traits were dubbed “magic traits” by Sergey Gavrilets in Gavrilets 2004 (cited in General Overviews of Speciation) because they automatically (i.e., magically) link assortative mating (and premating isolation) to adaptive divergence. Dieckmann and Doebeli 1999 develops an influential model that includes magic traits, and Merrill, et al. 2012 presents compelling empirical evidence for magic traits. Servedio, et al. 2011 reviews the state of evidence and addresses some controversies associated with magic traits.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–357.

Although somewhat contentious, this paper provides important theory behind sympatric speciation through resource competition. The results are robust with respect to many parameters and show sympatric speciation resulting from resource competition, even if assortative mating depends on an ecologically neutral marker trait. The authors provide many empirical studies to support their theoretical results, and propose that the nature of this mechanism for speciation is most likely during colonization events.

Merrill, R. M., R. W. R. Wallbank, V. Bull, et al. 2012. Disruptive ecological selection on a mating cue. *Proceedings of the Royal Society of London B: Biological Sciences* 279:4907–4913.

The authors put out into nature over a thousand model butterflies and also did an aviary experiment with live butterflies to show that bird predation generates selection against hybrids of two species of butterfly. This powerful empirical study provides good evidence that in this system, wing color patterns act as a “magic trait” in that they are both ecologically selected and used as a mate recognition cue.

Servedio, M. R., G. S. van Doorn, M. Kopp, A. M. Frame, and P. Nosil. 2011. Magic traits in speciation: “Magic” but not rare? *Trends in Ecology and Evolution* 26:389–397.

This highly cited review paper made an important step forward in resolving the controversy by clarifying what constitutes a “magic trait” and then evaluating available evidence and finding that these traits commonly contribute to speciation.

Mechanisms That Cause Female Preferences and Male Traits to Diverge

Identifying the nature of selection that causes divergence in mating preferences and male mating traits is an important research focus because it takes the study of speciation from describing patterns to revealing the selective mechanisms involved. Unfortunately, few studies focus on the evolution of mate preference, so clearly more work is needed here. We know more about how and why male mating traits evolve.

Sensory Drive

Sensory drive is probably the mechanism with the most support, and is one of the few hypotheses that have been tested for both signals and preference (Boughman 2001; Boughman 2002; Seehausen, et al. 2008; Tobias, et al. 2010). Sensory drive is an evolutionary process in which perceptual systems and communication signals adapt to local signaling environments, which in turn, causes preferences for mating signals and then the signals themselves to evolve as a byproduct of this adaptation. Sexual isolation is a natural outcome when populations inhabit different signaling environments. Because differences in habitat are common and the divergent adaptation that arises is intimately linked to premating isolation, sensory drive is very likely to play an important role in speciation for many taxa.

Boughman, J. W. 2001. Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature* 411:944–948.

This paper is one of the first studies to show that sexual isolation strengthens when male mating traits diverge in response to divergent female preferences that are in turn, related to differences in female perceptual abilities that have adapted to different environments.

Boughman, J. W. 2002. How sensory drive can promote speciation. *Trends in Ecology and Evolution* 17:571–577.

This review describes how this widespread adaptive process can have large effects on sexual isolation and sexual selection through the effects of signaling environments on both detection and discrimination of mating signals.

Kawata, M., A. Shoji, S. Kawamura, and O. Seehausen. 2007. A genetically explicit model of speciation by sensory drive with a continuous population in aquatic environments. *BMC Evolutionary Biology* 7:99.

This modeling paper shows that sensory drive (here, visual adaptation to heterogeneous habitats) can give rise to reproductive isolation in sympatry. The model assumptions are clearly given and directly based on explicit genetic mechanisms for color vision and nuptial coloration of a natural system (fish), making the paper accessible to a non-theoretical audience. The paper is an excellent example of a direct test of whether and how a suspected mode of speciation found in nature may work.

Seehausen, O., Y. Terai, I. S. Magalhaes, et al. 2008. Speciation through sensory drive in cichlid fish. *Nature* 455:620–626.

This elegant and highly cited study combines ecological, behavioral, perceptual, and molecular data to show that speciation is caused by sensory drive for a group of cichlid species from Lake Victoria in Africa.

Tobias, J. A., J. Aben, R. T. Brumfield, et al. 2010. Song divergence by sensory drive in Amazonian birds. *Evolution* 64:2820–2839.

Most studies of sensory drive in speciation focus on visual signals. This study of acoustic signals compares birds in two habitats and finds that song structure differs between habitats in ways that can be predicted by sound transmission properties of those habitats in addition to effects of size and bill morphology, while ruling out genetic differences or drift. The paper offers only an indirect connection to speciation.

Other Mechanisms

A number of mechanisms other than sensory drive have been proposed, but are less well studied. Example papers exploring each are listed in this section. These include selection for signaling performance (Derryberry, et al. 2012), sexual selection against hybrids (Naisbit, et al. 2001), divergent as opposed to strong mate preference (Rodríguez, et al. 2013), and good genes sexual selection (Welch 2003).

Debelle, A., M. G. Ritchie, and R. R. Snook. 2014. Evolution of divergent female mating preference in response to experimental sexual selection. *Evolution* 68:2524–2533.

Using experimental evolution lines of *Drosophila pseudoobscura* that vary in the strength of sexual selection they experience, this study demonstrates divergent evolution of female preferences that match previously characterized divergent evolution of male traits. The authors have a very interesting discussion of the hypothesized mechanisms driving this divergent selection.

Derryberry, E. P., N. Seddon, S. Claramunt, et al. 2012. Correlated evolution of beak morphology and song in the neotropical woodcreeper radiation. *Evolution* 66:2784–2797.

Testing the influence of ecological adaptation to signal production, these authors find that performance trade-offs in singing contribute to the diversification of song in a large clade of neotropical birds that do not learn their song. As beak shape and size evolve to improve feeding, the pitch and rate of song production is affected, which is expected to contribute to premating isolation and thus speciation.

Naisbit, R. E., C. D. Jiggins, and J. Mallet. 2001. Disruptive sexual selection against hybrids contributes to speciation between *Heliconius cydno* and *Heliconius melpomene*. *Proceedings of the Royal Society of London B: Biological Sciences* 268:1849–1854.

This study shows that sexual selection can act against hybrids, limiting gene flow and contributing to isolation. Thus sexual selection affects not only premating isolation but also postmating isolation.

Rodríguez, R. L., J. W. Boughman, D. A. Gray, E. A. Hebets, G. Höbel, and L. B. Symes. 2013. Diversification under sexual selection: The relative roles of mate preference strength and the degree of divergence in mate preferences. *Ecology Letters* 16:964–974.

A key prediction of speciation by sexual selection is that female preferences cause evolutionary change in male mating traits. This paper combines data from eight different taxonomic groups to test this prediction and presents the important finding that it is divergence in mate preferences, not the strength of those preferences, that determines how much evolutionary divergence occurs in male mating traits.

Svensson, E. I., and T. P. Gosden. 2007. Contemporary evolution of secondary sexual traits in the wild. *Functional Ecology* 21:422–433.

This paper reviews evidence for recent and rapid evolutionary change in secondary sexual traits, focusing primarily on morphological traits, and concludes that despite their role in sexual selection, contemporary evolution is more likely due to natural than to sexual selection, or to a change in the balance of the two. However, the paper does not cover male behavioral traits involved in mating, or the evolution of female preference, where sexual selection could be expected to play a more prominent role.

Welch, A. M. 2003. Genetic benefits of a female mating preference in gray tree frogs are context-dependent. *Evolution* 57:883–893.

Though not well studied, the possibility that female preferences diverge because of good genes sexual selection is suggested by this powerful study that used a split clutch design. The author found that genetic benefits of mate choice varied in two environments. Thus, mate preference would be expected to differ for populations inhabiting those distinct environments.

Evolving Isolating Barriers by Sexual Selection

Sexual selection can cause the evolution of several reproductive barriers. The most often considered is sexual isolation, and many of the papers in this section explore whether and how this barrier evolves (Boughman, et al. 2005; Gray and Cade 2000; Mendelson, et al. 2014; Ridgway and McPhail 1984). However, postmating mechanisms can also be influenced by sexual selection, when sexual selection acts against hybrids, as in flycatchers (Svedin, et al. 2008), sticklebacks (Vamosi and Schluter 1999), and butterflies (Naisbit, et al. 2001, cited in Mechanisms That Cause Female Preferences and Male Traits to Diverge: Other Mechanisms).

Boughman, J. W., H. D. Rundle, and D. Schluter. 2005. Parallel evolution of sexual isolation in sticklebacks. *Evolution* 59:361–373.

Using the concept of parallel speciation to study the evolution of sexual isolation, and comparing ecological and mating traits, this paper discriminates between ecological and non-ecological sexual and natural selection. It finds strong evidence that sexual isolation evolves in correlation with environment, ruling out drift and arbitrary sexual selection. Thus mating traits are more likely to track ecological traits under divergent natural selection, linking assortative mating and adaptive divergence and thus facilitating speciation.

Gray, D. A., and W. H. Cade. 2000. Sexual selection and speciation in field crickets. *Proceedings of the National Academy of Sciences of the United States of America* 97:14449–14454.

In one of the first studies about whether sexual selection is important early or late in the speciation process, the authors test whether sexual selection evolves through reinforcement (where selection against hybrids favors increased premating isolation). Instead, they find strong premating isolation with almost no postmating isolation, suggesting that sexual selection initiates divergence in mating traits and causes isolation before appreciable genetic differentiation has accumulated.

Mendelson, T. C., M. D. Martin, and S. M. Flaxman. 2014. Mutation-order divergence by sexual selection: Diversification of sexual signals in similar environments as a first step in speciation. *Ecology Letters* 17:1053–1066.

This paper introduces the “mutation-order” model of speciation via sexual selection—that two populations find different ways to adapt to initially similar sexual (perceptual) fitness landscapes. It includes verbal and mathematical models of the idea and a conceptual plan of action for future empirical tests of this idea; however, be prepared for a very complicated read.

Ridgway, M. S., and J. D. McPhail. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): Mate choice and reproductive isolation in the Enos Lake species pair. *Canadian Journal of Zoology* 62:1813–1818.

This now classic paper documents nearly perfect premating isolation in a species pair of stickleback fish inhabiting a single lake. Additional studies on this pair of species also demonstrates postmating isolation that depends on ecology, and other forms of isolation, including habitat and temporal isolation. However, sexual isolation is especially strong, showing its importance in the speciation process.

Svedin, N., C. Wiley, T. Veen, L. Gustafsson, and A. Qvarnström. 2008. Natural and sexual selection against hybrid flycatchers. *Proceedings of the Royal Society of London B: Biological Sciences* 275:735–744.

This study used a monumental twenty-four-year dataset and compared hybrids of pied and collared flycatchers to purebred males expressing intermediate plumage, to tease apart the effects of sexual selection and natural selection against hybrid flycatchers. The authors suggest that 74 percent of the reduction in fitness in hybrids is attributable to sexual selection. Despite the incredibly large dataset, the sample sizes used in these particular tests were extremely small, highlighting the difficulty of testing this question in nature.

Vamosi, S., and D. Schluter. 1999. Sexual selection against hybrids between sympatric stickleback species: Evidence from a field experiment. *Evolution* 53:874–879.

An early test of how sexual selection can act against hybrids, this study finds that F1 hybrids of limnetic and benthic sticklebacks had lower mating success when in competition with pure limnetic fish in outdoor enclosures. Although the process of reinforcement is not the focus of this study, the highlighting of a rarely considered source of hybrid inviability adds to the ways in which reinforcement could occur.

The Speciation Continuum: Sexual Selection, Hybridization, Extinction, and Reverse Speciation

Speciation is a dynamic process whereby a single species splits into two or more. The sequence is typically to go from a single variable interbreeding population, to differentiated populations that have reduced gene flow, to increasingly differentiated populations that have no gene flow and are thus fully isolated. Populations can be anywhere along this continuum, from having no reproductive isolation to being fully

isolated. Barton and de Cara 2009 develops a sophisticated model of how reproductive isolation evolves from weak to strong levels, incorporating coupling between multiple isolating mechanisms. Typically we think of species moving forward, where as time passes, reproductive isolation increases, but the process can also move backward, where partially isolated species start hybridizing, reducing differentiation and reproductive isolation (Taylor, et al. 2006). This process has been termed “reverse speciation,” meaning that the amount of reproductive isolation and the amount of differentiation are lessened. This term does not imply that the process is a mirror of exactly what happened in forward direction. The speciation process can also get stuck along the way—such that populations are not fully isolated (Nosil, et al. 2009). Given that sexual selection can play a role in the accumulation of reproductive isolation and thus forward speciation, questions are raised about its potential role in the speciation continuum and reverse speciation. Several studies demonstrate that it may be pivotal to the process (Seehausen, et al. 1997; Lackey and Boughman 2013). In certain circumstances hybridization can be adaptive because it produces offspring that have higher fitness than pure species, favoring flexible mate choice (Pfennig 2007). Another effect is that sexual selection may increase extinction rates, counteracting its diversifying effect on speciation (Doherty, et al. 2003).

Barton, N. H., and M. A. R. de Cara. 2009. The evolution of strong reproductive isolation. *Evolution* 63:1171–1190.

This paper models multiple incompatibilities and how they may act together to increase reproductive isolation from initially low levels. The authors argue that pre- and post-zygotic incompatibilities can cause strong isolation when coupled, and provide an important mechanism by which assortment can arise through associations with other components of reproductive isolation. This extremely thorough theory paper also directly addresses parapatric speciation, which is often treated as a special condition of allopatric and sympatric speciation.

Doherty, P. F., G. Sorci, J. A. Royle, J. E. Hines, J. D. Nichols, and T. Boulinier. 2003. Sexual selection affects local extinction and turnover in bird communities. *Proceedings of the National Academy of Sciences of the United States of America* 100:5858–5862.

Although sexual selection may enhance speciation, costs of extravagant ornaments may also increase extinction. Few comparative studies have explored these effects on population persistence and overall diversification rates. This influential study uses data on bird populations, finding that dichromatic species are more likely to go locally extinct, but also have higher turnover rates. The interplay between local extinction and recolonization results in relatively stable numbers of dichromatic species in local communities.

Garner, S. R., and B. D. Neff. 2013. Alternative male reproductive tactics drive asymmetrical hybridization between sunfishes (*Lepomis* spp.). *Biology Letters* 9:20130658.

This study determines through paternity analysis that males of one species of fish that adopt a sneaker strategy are driving asymmetric hybridization with a second species. Despite a large fitness disadvantage to hybridization, sneaker males may still be sexually selected to spawn in heterospecific nests if their only other option is to have zero fitness. This intriguing result suggests that sexual selection can sometimes favor hybridization.

Lackey, A. C. R., and J. W. Boughman. 2013. Loss of sexual isolation in a hybridizing stickleback species pair. *Current Zoology* 59:591–603.

Documenting reverse speciation is a first step, but raises questions about which isolating mechanisms are lost, thus allowing for hybridization. This study compares data from before and after hybridization ensued in a British Columbia species pair of sticklebacks to show that sexual isolation was weakened.

Merrill, R. M., Z. Gompert, L. M. Dembeck, M. R. Kronforst, W. O. McMillan, and C. D. Jiggins. 2011. Mate preference across the speciation continuum in a clade of mimetic butterflies. *Evolution* 65:1489–1500.

This paper explores how sexual selection enhances speciation across a continuum of divergence in *Heliconius* butterflies, comparing polymorphisms within a single population to “good” biological species with near-complete reproductive isolation. This comparison reveals that sexual isolation evolves very early and continues to strengthen throughout the process of speciation. The powerful approach taken and the strong support for an early role of mate-preference evolution in speciation make this paper stand out.

Nosil, P., L. J. Harmon, and O. Seehausen. 2009. Ecological explanations for (incomplete) speciation. *Trends in Ecology and Evolution* 24:145–156.

This review outlines ecological processes that can keep speciation from going to completion. It considers how the likelihood of speciation is affected by strong selection on a few loci and traits, versus selection acting on many loci and traits, thus involving much of the genome.

Pfennig, K. S. 2007. Facultative mate choice drives adaptive hybridization. *Science* 318:965–967.

This influential study shows that hybridization can occasionally be adaptive under specific environmental conditions, and that females can alter their mate choice to favor heterospecific mates under such conditions.

Seehausen, O., J. M. M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277:1808–1811.

When the traits used to distinguish between conspecific and heterospecific mates are obscured, hybridization rates between sympatric species are likely to increase. This highly cited study shows that species diversity is reduced in turbid water, implicating sexual selection in the maintenance of species boundaries.

Stelkens, R. B., M. E. Pierotti, D. A. Joyce, A. M. Smith, I. van der Sluijs, and O. Seehausen. 2008. Disruptive sexual selection on male nuptial coloration in an experimental hybrid population of cichlid fish. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:2861–2870.

Based on an underutilized approach of using lab-generated hybrids between two differently colored species of cichlid fish, this study demonstrates that divergent female choice by each of the pure species generates disruptive selection on male color. The authors also find that F2 female hybrids generate disruptive selection on male color, suggesting a genetic basis for red and blue color preferences.

Taylor, E. B., J. W. Boughman, M. Groenenboom, M. Sniatynski, D. Schluter, and J. L. Gow. 2006. Speciation in reverse: Morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. *Molecular Ecology* 15:343–355.

One of the iconic species pairs of threespine sticklebacks from British Columbia began hybridizing at high rates, reversing the speciation process. This study is one of the first to document this process in nature with both morphological and genetic data from museum collections and wild-caught fish.

The Role of Sexual Selection in Sympatric Speciation

Across geographic contexts, the role that sexual selection plays in speciation may differ. However, as addressed by Bolnick and Fitzpatrick 2007, our ability to understand sympatric speciation in the past is limited due to biogeographic changes that have may have occurred since speciation happened. This limitation has posed a challenge for both empiricists to catch speciation in action, and for theoreticians to consider geography and habitat-specific conditions as they model how sympatric speciation can occur. Some models have explored the importance of the physical environment (particularly in how it affects female ability to discriminate signals; Higashi, et al. 1999), whereas others contend that the *social* environment plays a larger role (Kirkpatrick and Nuismer 2004; van Doorn, et al. 2004; Servedio 2011). A key point is to understand why disruptive sexual selection should initially occur, and whether this is linked to or independent of natural selection. While van Doorn, et al. 2004 suggest frequency-dependent female preferences could generate disruptive selection, Kirkpatrick and Nuismer 2004 find that speciation is impeded when rare phenotypes have difficulty finding compatible partners. Other papers have directly addressed the extent of assortative mating in speciation, particularly how much is needed to start and continue the speciation process (Servedio 2011). Some papers cast doubt on whether sexual selection does play a direct role (Arnegard and Kondrashov 2004; van Doorn, et al. 2004). We still have few studies that marry the empirical and theoretical evidence for speciation by sexual selection, and need direct tests of the theories to identify which factors are most important in determining the likelihood of sympatric speciation by sexual selection.

Arnegard, M. E., and A. S. Kondrashov. 2004. Sympatric speciation by sexual selection alone is unlikely. *Evolution* 58:222–237.

This theory paper links genetic variability to the long-term stability of speciation via sexual selection. The authors test several models and conclude that preferences for extreme displays are unlikely to cause sympatric speciation and more likely to evolve under disruptive natural selection. This paper expands and tests the conditions of prior speciation-by-sexual-selection models, connects theory to African cichlid diversity, and aptly addresses limitations that should serve as goals for future work.

Bolnick, D. I., and B. M. Fitzpatrick. 2007. Sympatric speciation: Models and empirical evidence. *Annual Review of Ecology, Evolution, and Systematics* 38:459–487.

Sympatric speciation is highly contentious, and this review paper does an excellent job addressing whether theoretical assumptions are met in nature. In addition to a historical introduction, it elucidates the causes of disruptive selection, and current empirical support. It highlights that sympatric speciation may seem uncommon, but the geographic context of past speciation will be difficult to resolve because of biogeographic changes. This is a good introduction to sympatric speciation, and raises unresolved questions.

Higashi, M., G. Takimoto, and N. Yamamura. 1999. Sympatric speciation by sexual selection. *Nature* 402:523–526.

This theory paper describes how the ability to distinguish mating trait variants and the costs associated with conspicuous signaling can influence sympatric speciation. The model proposes divergent runaway processes in male traits, and suggests that speciation should be more common when predation pressure is reduced and in habitats with high signal transmission, suggesting that speciation depends on environmental integrity. It requires stringent conditions; however, raising subsequent questions about how commonly the process occurs.

Kirkpatrick, M., and S. L. Nuismer. 2004. Sexual selection can constrain sympatric speciation. *Proceedings of the Royal Society of London B: Biological Sciences* 271:687–693.

Although many models of sympatric speciation assume that individuals have equal mating success and mate assortatively, this theory paper considers that, in nature, rare phenotypes often have lower mating success because of the struggle to find compatible partners, and stabilizing selection against these rare types can impede speciation. This paper is particularly valuable in noting the limits of models and enumerating specific gaps in our empirical knowledge of stabilizing selection and assortative mating in sympatric speciation.

Servedio, M. R. 2011. Limits to the evolution of assortative mating by female choice under restricted gene flow. *Proceedings of the Royal Society of London B: Biological Sciences* 278:179–187.

This theory paper explores how the existence of assortative mating drives its further evolution. The model considers local adaptation and different genetic architectures of traits and importantly finds that assortment via sexual selection may be limited to an intermediate value, but may interact in significant ways with other factors, such as search costs and fundamental factors in premating isolation. This paper is an excellent example of testing basic assumptions made in modeling sympatric speciation.

van Doorn, G. S., U. Dieckmann, and F. J. Weissing. 2004. Sympatric speciation by sexual selection: A critical reevaluation. *American Naturalist* 163:709–725.

This theory paper is important because it narrows the scope of when sexual selection is likely to result in speciation. In particular, the authors provide a previously lacking adaptive mechanism that the frequency dependence of female preference gives rise to stable variation via disruptive selection. The article begins with a nice overview of previous models, and its discussion is a must-read to relate, compare, and contrast the multiple, simultaneously acting mechanisms that may restrict adaptive speciation to prior models of sympatric speciation by sexual selection.

Reinforcement and Sexual Selection

The basic idea of reinforcement is that selection against hybrids should generate selection on enhanced premating isolation. Reinforcement was controversial until a series of theoretical models demonstrated the fairly broad conditions under which it could occur, and empirical studies began to find supporting evidence (reviewed in Servedio and Noor 2003; Ortiz-Barrientos, et al. 2009). A key premating mechanism is sexual isolation; therefore, sexual selection could be central to whether and how this process works. Early studies have shown the predicted increase in assortative mating (e.g., Noor 1995, Rundle and Schluter 1998). A series of theoretical models have explored the conditions when sexual selection does and does not contribute (e.g., Servedio 2001, Servedio 2004). Some more recent work explores the potential for reinforcement to lead to further diversification: sympatric populations experiencing divergence through reinforcement may also diverge from their allopatric congeners to the extent that mating between them would be significantly reduced if they had secondary contact (Hoskin, et al. 2005), thus resulting in three or more incipient species. This process has been called “cascade reinforcement,” and is likely driven by sexual selection.

Hoskin, C. J., M. Higgle, K. R. McDonald, and C. Moritz. 2005. Reinforcement drives rapid allopatric speciation. *Nature* 437:1353–1356.

This paper is one of the first empirical tests of the “cascade reinforcement” hypothesis.

Noor, M. A. F. 1995. Speciation driven by natural selection in *Drosophila*. *Nature* 375:674–675.

This classic paper is one of the very first empirical studies documenting support for reinforcement and was written at a time when the hypothesis was still controversial.

Ortiz-Barrientos, D., A. Grealy, and P. Nosil. 2009. The genetics and ecology of reinforcement: Implications for the evolution of prezygotic isolation in sympatry and beyond. *Annals of the New York Academy of Sciences* 1168:156–182.

The authors provide a detailed review linking newer empirical studies about reinforcement’s role in speciation, and define five key areas of future research, particularly as related to the relative importance of between- and within-species sexual selection to other forces. They also consider the genetics of preference and articulate the “cascade reinforcement” hypothesis. In addition, the paper includes very helpful comparative tables and figures that nicely illustrate the finer points of speciation through prezygotic isolation.

Rundle, H. D., and D. Schluter. 1998. Reinforcement of stickleback mate preferences: Sympatry breeds contempt. *Evolution* 52:200–208.

An important experimental study that demonstrates reproductive character displacement by comparing mate preferences of female benthic sticklebacks from a lake with benthic and limnetic sticklebacks to those of female benthic sticklebacks from single-species lakes. Although on its own not evidence for reinforcement, the study is strongly suggestive, given that it was previously shown that hybridization has occurred in the past between benthic and limnetic fish and these hybrids have lower fitness.

Servedio, M. R. 2001. Beyond reinforcement: The evolution of premating isolation by direct selection on preferences and postmating, prezygotic incompatibilities. *Evolution* 55:1909–1920.

Enhanced assortative mating on secondary contact may arise through mechanisms other than classical reinforcement. Here, the author models direct selection acting against females who choose heterospecific mates and compares its effect to selection against hybrids. Direct selection is found to be more powerful, and thus may be more likely.

Servedio, M. R. 2004. The evolution of premating isolation: Local adaptation and natural and sexual selection against hybrids. *Evolution* 58:913–924.

This theory paper examines whether selection against hybrids or local adaptation results in stronger assortative mating. This result depends on whether preferences act directly or indirectly on loci affecting hybrid fitness. Under many conditions, preference for locally adapted males will be stronger. However, pleiotropy between hybrid fitness and female choice results in faster evolution of premating isolation. This work addresses the shortfalls of weak selection commonly assumed in models, and compares alternative models.

Servedio, M. R., and M. A. F. Noor. 2003. The role of reinforcement in speciation: Theory and data. *Annual Review of Ecology, Evolution, and Systematics* 34:339–364.

Following substantial progress showing that reinforcement can occur, this review focuses on its frequency and importance in speciation. The review covers the evolution of incompatibilities, mechanisms of nonrandom mating, geographic effects, and the nature of mating traits and their genetic basis. The paper calls for more holistic investigations of isolation in nature, a better understanding of migration rates and asymmetries in reinforcement, and the use of more distantly related species.

Male Competition and Male Mate Choice also Contribute to Speciation

Darwin 1871 (cited in the Early History of Sexual Selection and Speciation) describes two processes that came to influence reproductive success: intersexual choice (often females choosing males) and intrasexual competition (often male-male). The latter process has received much less attention in speciation research than the former. West-Eberhard 1983 (cited in the Early History of Sexual Selection and Speciation) highlights the potential importance of intrasexual competition in speciation. However, the idea lay dormant until recently. Seehausen and Schluter 2004 suggested male-male competition could be responsible for divergent selection on male coloration in cichlids. Specifically, negative frequency-dependent selection on male color could result from males directing aggression toward males with similar coloration, and Seehausen and Schluter 2004 presents correlative data to support this hypothesis. However, experimental data from cichlids is less clear, with the stage of speciation having a large influence on whether males bias aggression toward males of the same color (Dijkstra, et al. 2007), and aggression bias alone may be unlikely to push sympatric speciation to completion. Strongly inspired by this work in cichlids, van Doorn, et al. 2004 (cited in the Role of Sexual Selection in Sympatric Speciation) provides theoretical support for male-male competition being important in speciation, finding that male-male competition based on traits also under female choice increases the likelihood of sympatric speciation. In a slightly different vein, other researchers have studied how intrasexual selection may influence the completion of speciation following secondary contact by formerly allopatric incipient species (Grether, et al. 2009, Anderson and Grether 2010). The broad conclusion from this work is that male-male competition can have important effects on speciation. Qvarnström, et al. 2012 is a very approachable review of this work. Male-male competition remains a neglected area of research, however, and many critical questions remain. For example, are alternative reproductive strategies and incipient species different sides of the same coin? Is negative frequency-dependent selection the only way novel male traits can invade a population? How do the different types of sexual selection (male competition and female choice) interact? Even less studied than the effect of male-male competition is how male mate choice may affect the speciation process. Several modeling papers explore the dynamics of the evolution of male mate choice and discuss how it might impact speciation, especially with respect to assortative mating (Servedio and Lande 2006, Servedio 2007). These papers have generally found the conditions supporting the evolution of male mate choice are fairly restrictive. There have been very few empirical studies; two illuminating examples are Kozak, et al. 2009 and Svensson, et al. 2007. Interestingly, the first finds that males are not very choosy and their actions would inhibit speciation, whereas the second finds that males are especially choosy and their actions would strongly promote speciation. Thus, how important male mate choice is in the speciation process remains to be tested with further theoretical and empirical work.

Anderson, C. N., and G. F. Grether. 2010. Interspecific aggression and character displacement of competitor recognition in *Hetaerina* damselflies. *Proceedings of the Royal Society of London B: Biological Sciences* 277:549–555.

This elegant empirical test of agonistic character displacement utilizes an experimental design of four damselfly species from allopatric or sympatric populations with a manipulative wing-color experiment to confirm their correlative results. The authors find strong evidence that in sympatry two different species show character displacement of competitor recognition such that they reduce competitive interactions with a third species, but are too similar in coloration to the fourth species for competitor recognition to shift.

Dijkstra, P. D., O. Seehausen, M. E. R. Pierotti, and T. G. G. Groothuis. 2007. Male-male competition and speciation: Aggression bias toward differently coloured rivals varies between stages of speciation in a Lake Victoria cichlid species complex. *Journal of Evolutionary Biology* 20:496–502.

This study finds ambiguous results testing for aggression bias in cichlid fish. Blue fish from single (blue) species or sister-pair species (blue and red) directed aggression toward blue compared to red fish, but this was not the case in hybridizing species. Unfortunately, the authors do not present a convincing hypothesis for these puzzling reversals in color-biased aggression along the speciation continuum.

Grether, G. F., N. Losin, C. N. Anderson, and K. Okamoto. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biological Reviews* 84:617–635.

This comprehensive review focuses on agonistic character displacement (both divergent and convergent), defined as an evolutionary shift in either agonistic signal and/or competitor recognition, resulting from intrasexual interference competition in secondary contact. This is primarily an empirical review, but it opens with an individual-based model to confirm conditions under which competitor recognition and agonistic signals are expected to evolve after secondary contact.

Kozak, G. M., M. Reiland, and J. W. Boughman. 2009. Sex differences in mate recognition and conspecific preference in species with mutual mate choice. *Evolution* 63:353–365.

When both sexes express preferences it becomes less clear whether male or female choice will be most important for maintaining reproductive isolation. This is one of very few studies that tested both male and female choice in a system with mutual mate choice. Although males can discriminate between con- and heterospecific females, they court both species with equal vigor, which would undermine isolation. In contrast, females have very strong preferences for conspecifics and almost always reject heterospecific males.

Qvarnström, A., N. Vallin, and A. Rudh. 2012. The role of male contest competition over mates in speciation. *Current Zoology* 58:493–509.

A very readable and up-to-date review of how male-male competition can influence the speciation process. The authors conclude that male-male competition can play a critical role in speciation and they call for more studies that focus on male-male competition but also on the interaction between natural and sexual selection (rather than their independent contribution) in the process of speciation.

Seehausen, O., and D. Schluter. 2004. Male-male competition and nuptial-colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proceedings of the Royal Society of London B: Biological Sciences* 271:1345–1353.

The authors propose the novel hypothesis that male-male competition could lead to disruptive selection on color through differential male aggression toward other males with similar color patterns and present correlative evidence in cichlid fish. They also provide a verbal model for how negative frequency-dependent selection through male competition may interact with female preference evolution to ultimately result in sympatric speciation, which to our knowledge, remains untested.

Servedio, M. R. 2007. Male versus female mate choice: Sexual selection and the evolution of species recognition via reinforcement. *Evolution* 61:2772–2789.

This theory paper establishes how selection (directly and indirectly) acts on male versus female preferences for traits that increase viability, and the likelihood that male mate choice evolves under reinforcement. The models find that male preferences tend to be selected against unless females vary in quality (i.e., fecundity) and, importantly, that reinforcement may occur via male mate choice alone, although is more likely with female mate choice because it more easily evolves.

Servedio, M. R., and R. Lande. 2006. Population genetic models of male and mutual mate choice. *Evolution* 60:674–685.

Male and mutual mate choice are investigated to complement previous models of female preferences alone. The authors test a series of conditions and summarize their findings with respect to the maintenance or loss of male preference. This paper incorporates fertility, courtship output, and pleiotropy into models of sexual selection, and suggests conditions under which the maintenance of male-trait polymorphisms (and assortative mating based on these traits) may initiate the speciation process.

Svensson, E. I., K. Karlsson, M. Friberg, and F. Eroukhanoff. 2007. Gender differences in species recognition and the evolution of asymmetric sexual isolation. *Current Biology* 17:1943–1947.

This elegant empirical paper experimentally manipulates wing color in damselflies and shows that both males and females of two sympatric species can discriminate between the two species. A novel finding is that males of the dark-winged species have evolved stronger mate recognition than females, resulting in an extreme reduction in courtship attempts on heterospecific females.

Sexual Conflict and Speciation

Sexual conflict is generated when the reproductive interests of males and females differ, resulting in different fitness optima. This is often the case in polygynous systems, and results in a coevolutionary process whereby each sex exerts selection on reproductive traits in the other sex, causing rapid and perpetual evolutionary change. Even the early work on sexual conflict recognized its potential for speciation (Parker 1979, Parker and Partridge 1998). Evidence in support includes comparative work (Arnqvist, et al. 2000), experimental evolution (Martin and Hosken 2003, Martin and Hosken 2004), and formal and verbal theory (Gavrillets 2000, Gavrillets and Waxman 2002, Bonduriansky 2011). Clear links between theory and empirical evidence are still needed.

Arnqvist, G., M. Edvardsson, U. Friberg, and T. Nilsson. 2000. Sexual conflict promotes speciation in insects. *Proceedings of the National Academy of Sciences of the United States of America* 97:10460–10464.

This seminal study takes a powerful comparative approach to show that taxa with the opportunity for strong postmating sexual conflict have more species than those with low opportunity for postmating conflict.

Bonduriansky, R. 2011. Sexual selection and conflict as engines of ecological diversification. *American Naturalist* 178:729–745.

This thoughtful paper considers how sexual selection and sexual conflict could directly foster ecological divergence and speciation. The author uses fitness landscapes and the countervailing effects of sexual and natural selection to outline how sexual selection and sexual conflict could move populations away from a viability optimum (or fitness peak), into the “range of attraction” of a new peak. Doing so could result in populations evolving to fill a novel ecological niche.

Gavrillets, S. 2000. Rapid evolution of reproductive barriers driven by sexual conflict. *Nature* 403:886–889.

How antagonistic coevolution of male and female traits by sexual conflict can lead to divergence and speciation is addressed in this theory paper. Continual changes in male and female mating traits can cause genetic divergence, reproductive incompatibility, and reproductive isolation. In resource-rich environments, populations reach higher density and large populations enhance effects because selection is more efficient and sexual conflict is stronger. Such conditions should be relatively common.

Gavrillets, S., and D. Waxman. 2002. Sympatric speciation by sexual conflict. *Proceedings of the National Academy of Sciences of the United States of America* 99:10533–10538.

The authors model the link between sexual conflict and speciation. This paper describes distinct ways that conflict between males and females may lead to speciation, which are not based on the classic Fisherian runaway scenario that underlies many speciation models. Females may escape the burden of sexual conflict through diversification and speciation, predicting that female alleles will be more diverse than those of males.

Martin, O. Y., and D. J. Hosken. 2003. The evolution of reproductive isolation through sexual conflict. *Nature* 423:979–982.

This empirical paper provides experimental evidence that increased population size and density increases sexual conflict and thereby behavioral reproductive isolation. This paper is important for confirming the alternative, contentious theory that divergence is more likely in larger populations because of sexual conflict, rather than in smaller population, as classical population genetics theory would suggest. Additionally, the paper proposes an important link between speciation and population inbreeding and genetic variation.

Martin, O. Y., and D. J. Hosken. 2004. Reproductive consequences of population divergence through sexual conflict. *Current Biology* 14:906–910.

The authors use experimental evolution to investigate the consequences of sexual conflict in speciation. By comparing populations evolved with varying levels of conflict, the paper shows that sexual conflict can lead to reduced mating between populations, showing that conflict contributes to reproductive isolation. It also demonstrates that such conflict creates a selective load.

Parker, G. A. 1979. Sexual selection and sexual conflict. In *Sexual Selection and Reproductive Competition in Insects*. Edited by M. S. Blum and N. A. Blum, 123–166. New York: Academic Press.

This seminal work is one of the first to describe sexual conflict. It provides both verbal and mathematical models to show the relative costs and benefits of reproductive traits in males and females may differ, and this imbalance can cause evolutionary change.

Parker, G. A., and L. Partridge. 1998. Sexual conflict and speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 353:261–274.

This paper is one of the first to articulate the connection between sexual conflict and speciation. The theoretical models rely on female choice in determining the likelihood of interpopulation matings and reinforcement, and predict that when the balance is tipped in favor of females, higher rates of speciation will result through premating isolation, and populations will be less genetically diverse.

Postcopulatory Sexual Selection and Speciation

Increasingly, scientists are recognizing the potential for sexual selection after mating to influence fertilization, and thus gene flow between species, although the impact on isolation of these postcopulatory mechanisms is less well studied than premating mechanisms. Effects can occur through mechanisms of cryptic mate choice, competition among sperm or pollen from con- and heterospecific mates, and interactions among male and female gametes. Whenever conspecifics are favored, isolation between species is enhanced—for example, when conspecific sperm or pollen is more likely than heterospecific sperm or pollen to fertilize eggs (termed conspecific sperm precedence)—as found in both animals (Immler, et al. 2011) and plants (Rieseberg, et al. 1995). Although it has repeatedly been found, and intuitively makes sense, some theoretical work in Lorch and Servedio 2007 suggests conspecific sperm precedence might have a limited effect on speciation, at least in the context of secondary contact and reinforcement. That females can manipulate fertilizations initially surprised the scientific community, but the wealth of evidence shows such control to be widespread. Many of the mechanisms that affect isolation between species may derive from sperm competition within species, suggested in the review Birkhead and Brillard 2007 and tested by Immler, et al. 2011. When sperm competition is intense, factors that influence whether conspecific males have higher fertilization success can have a large impact on hybridization. Even so, Yeates, et al. 2013 shows female traits mediate sperm competition, and reduces success of heterospecific sperm, preventing costly production of hybrid offspring. These ideas are appealing, but should not be taken on intuition alone, as evidenced by an intriguing study on genital morphology and hybridization in *Drosophila* reported by LeVasseur-Viens, et al. 2015.

Birkhead, T. R., and J.-P. Brillard. 2007. Reproductive isolation in birds: Postcopulatory prezygotic barriers. *Trends in Ecology & Evolution* 22:266–272.

This paper reviews potential ways in which postcopulatory prezygotic mechanisms can influence reproductive isolation in birds. Although the authors conclude that such mechanisms are inefficient in birds when compared to other taxa, they argue that postcopulatory sexual selection may have general importance because mechanisms like cryptic choice and sperm competition are so widespread in animal taxa, and may even be found in plants.

Immler, S., M. B. Hamilton, N. J. Poslusny, T. R. Birkhead, and J. M. Epifanio. 2011. Post-mating reproductive barriers in two unidirectionally hybridizing sunfish (Centrarchidae: *Lepomis*). *Journal of Evolutionary Biology* 24:111–120.

Two sunfish species are isolated, in part, by conspecific sperm precedence, but this factor acts only in one direction, thus helping to explain why hybridization appears to be asymmetric, allowing gene flow in one direction but preventing it in the other. These species also show premating isolation by both males and females, and some postmating hybrid inviability, highlighting that multiple barriers often contribute to speciation.

LeVasseur-Viens, H., M. Polak, and A. J. Moehring. 2015. No evidence for external genital morphology affecting cryptic female choice and reproductive isolation in *Drosophila*. *Evolution* 69:1797–1807.

Male genitalia are highly diverse among taxa, a pattern that is thought to reflect selection for fertilization through cryptic female choice and has implications for reproductive isolation. This popular concept has rarely been directly tested, however, and we need such tests of intuition. Surprisingly, this important paper refutes cryptic choice but instead supports premating mechanisms as the cause of genital evolution in *Drosophila*, and also shows that genital differences have little effect on reproductive isolation.

Lorch, P. D., and M. R. Servedio. 2007. The evolution of conspecific gamete precedence and its effect on reinforcement. *Journal of Evolutionary Biology* 20:937–949.

Following empirical work by these authors that showed only weak effects (counter to predictions of some theory), this model explores the evolution of both premating isolation and conspecific sperm precedence in the context of reinforcement. Although both can contribute to speciation, the model concludes that conspecific sperm precedence and reinforcement are mutually inhibitory, because each reduces selection that would favor the evolution of the other.

Rieseberg, L. H., A. M. Desrochers, and S. J. Youn. 1995. Interspecific pollen competition as a reproductive barrier between sympatric species of *Helianthus* (Asteraceae). *American Journal of Botany* 82:515–519.

This classic paper lays out the logic of pollen competition preventing interspecific hybridization in plants, and raises awareness of the similarity between sperm and pollen competition. It also presents empirical evidence in support of this mechanism in sunflowers.

Yeates, S. E., S. E. Diamond, S. Einum, B. C. Emerson, W. V. Holt, and M. J. G. Gage. 2013. Cryptic choice of conspecific sperm controlled by the impact of ovarian fluid on sperm swimming behavior. *Evolution* 67:3523–3536.

Working out the mechanistic basis of cryptic choice and conspecific sperm precedence is challenging, making such studies particularly valuable. This paper reports that ovarian fluid of trout and salmon, but not the egg itself, mediates fertilization success through effects on the swimming behavior and chemoattraction of conspecific sperm. Sperm are more attracted to and swim more directly to the egg in ovarian fluid of their own as compared to the other species.

Learning, Sexual Selection, and Speciation

Learning is a change in behavior based on previous experience. Interest in how learning can influence adaptation and evolution in general has spilled over to an interest in how it might influence the speciation process. Learning is particularly interesting because it can result both in plasticity and non-genetic inheritance of preferences or traits. Learning can have effects that either enhance or lessen the likelihood of

speciation, depending on various conditions. Thus far, research has primarily focused on how learning affects mate preferences. For example, Dukas and his colleagues have conducted many experiments in fruit flies on how learning influences assortative mating and biases both male courtship and female receptivity. A short review of this and other relevant work on learning and speciation is Dukas 2013. Irwin and Price 1999 is an early review of the potential importance of imprinting on speciation. This suggestion has been followed up more recently with modeling work by Verzijden, et al. 2005, which focuses on the more specific question of how imprinting might impact sympatric speciation, an area of particular interest to researchers because of the more stringent conditions under which it is likely to occur relative to speciation with limited or no gene flow. Two empirical studies of imprinting that stand out in the field are Kozak, et al. 2011, which demonstrates paternal imprinting in sticklebacks, and Westerman, et al. 2012, which demonstrates oblique imprinting, or change in preference because of experiences as immatures with individuals from the population at large (rather than, for example, a parent), in butterflies. Verzijden, et al. 2012 is an excellent place to start for a recent review of the theoretical and empirical work on how learned mate preferences and learned mating traits can affect speciation.

Dukas, R. 2013. Effects of learning on evolution: Robustness, innovation and speciation. *Animal Behaviour* 85:1023–1030.

This general review of how learning can influence evolution also includes a section on how learning can influence speciation. In the speciation section is a review of how learning can influence assortative mating through processes such as imprinting and trial-and-error learning over the course of successive courtship experiences.

Grant, B. R., and P. R. Grant. 2010. Songs of Darwin's finches diverge when a new species enters the community. *Proceedings of the National Academy of Sciences of the United States of America* 107:20156–20163.

Using data from the remarkable long-term study of Darwin's finches in the Galapagos Islands, the authors examine how established species respond to the arrival of a new, more dominant species. The authors find strong evidence that over three decades males of the resident species speeded up their trill rate through a peak shift mechanism whereby sons biased song learning away from the new species' song. Moreover, a new independent lineage was established through hybridization, with distinct song, behavior, and morphology.

Irwin, D. E., and T. D. Price. 1999. Sexual imprinting, learning and speciation. *Heredity* 82:347–354.

This review shifts the focus from genetic mechanisms contributing to speciation to the potential for learned mate choice and imprinting to increase reproductive isolation.

Kozak, G. M., M. L. Head, and J. W. Boughman. 2011. Sexual imprinting on ecologically divergent traits leads to sexual isolation in sticklebacks. *Proceedings of the Royal Society of London B: Biological Sciences* 278:2604–2610.

Imprinting will increase isolation, especially when young imprint on traits that are divergent adaptations. This experimental study uses a classical cross-fostering design to show that stickleback fish imprint on their fathers, cueing on color and odor, both of which are adaptations to the species' distinct environments.

Verzijden, M. N., R. F. Lachlan, and M. R. Servedio. 2005. Female mate-choice behavior and sympatric speciation. *Evolution* 59:2097–2108.

Using both population genetics models and individual-based simulations, the authors show that the details of how female preferences are determined have profound effects on the likelihood of sympatric speciation. Specifically, phenotype matching and maternal imprinting have nearly identical effects in strongly improving the likelihood of sympatric speciation, paternal imprinting makes sympatric speciation more difficult, and with oblique imprinting, sympatric speciation doesn't happen at all.

Verzijden, M. N., C. ten Cate, M. R. Servedio, G. M. Kozak, J. W. Boughman, and E. I. Svensson. 2012. The impact of learning on sexual selection and speciation. *Trends in Ecology and Evolution* 27:511–519.

Summarizing both theory and empirical data from a wide range of taxa, this highly cited review indicates that learning may play an especially important role in speciation, often fostering the process but occasionally counteracting it.

Westerman, E. L., A. Hodgins-Davis, A. Dinwiddie, and A. Monteiro. 2012. Biased learning affects mate choice in a butterfly. *Proceedings of the National Academy of Sciences of the United States of America* 109:10948–10953.

This study uses manipulative experiments to show that in female butterflies, premating experience before reproductive maturity changes an innate mating-preference bias. There is also some limited evidence that these butterflies learn preferences for signal enhancement more easily than preferences for signal reduction. Interestingly, this pattern makes it unlikely that the species studied would mate with its sympatric congeners, which have fewer spots.

Finding the Genetic Basis of Sexual Selection and Speciation

Evolution depends on both selection and heritability, making the study of the genetic basis of sexual isolation a key to understanding speciation. Many approaches can be used to gain insight into speciation genetics, including quantitative genetics, classical genetics, genomics, and gene expression work. However, this task is challenging to do for mating traits, especially behavioral traits like courtship behavior and mate preference; therefore, relatively few studies have been done. Nonetheless, a few seminal papers are beginning to shed light on the genetics of sexual selection and sexual isolation, and progress should hasten with the availability of genomics tools for non-model taxa. Included in this section are a few of the many papers in this field, divided by whether they are general reviews or focus on genetic architecture and gene finding.

Reviews

Classic reviews are listed here as a starting point. Coyne 1992 highlights the likely importance of premating barriers as a counterpoint to the great emphasis that much genetics of speciation places on postmating intrinsic barriers. Grant and Grant 1997 considers general ideas relevant to bird speciation, and Swanson and Vacquier 2002 explores sexual conflict and postmating isolation.

Coyne, J. A. 1992. Genetics and speciation. *Nature* 355:511–515.

This classic review explores the genetic basis of speciation, including the historically important theory and empirical work available at the time. Key questions are identified that continue to serve as drivers of research programs. The author points out that sexual isolation and other premating mechanisms are likely to be of particular importance.

Grant, P. R., and B. R. Grant. 1997. Genetics and the origin of bird species. *Proceedings of the National Academy of Sciences of the United States of America* 94:7768–7775.

This influential paper describes the challenges of uncovering the genetic basis of speciation in birds. Postmating isolation evolves quite late in many bird taxa, and instead reproductive isolation depends on sexual isolation through differences in plumage, morphology, courtship, mate choice, and song (affected by learning). The authors hypothesize that many of these traits will be polygenic. The potential for hybridization to facilitate subsequent speciation is also discussed, which is an influential, albeit controversial, idea.

Swanson, W. J., and V. D. Vacquier. 2002. The rapid evolution of reproductive proteins. *Nature Reviews Genetics* 3:137–144.

Research on sexual selection and speciation often focuses on female mate choice and male mating traits, but postcopulatory interactions between the sexes can also affect hybridization. These postcopulatory interactions will be governed by genes coding for reproductive proteins involved in sperm-egg interactions, “gamete recognition,” spermiogenesis, and other reproductive processes. This highly cited review describes evidence that genes coding for reproductive proteins evolve particularly rapidly, and such rapid evolution increases reproductive isolation between species.

Genetic Architecture and Gene Finding

Major efforts have been devoted to understanding the genetic architecture of speciation: for example, the distribution, effect sizes, and number of genetic regions that govern traits involved in reproductive isolation caused by sexual selection. Chenoweth and Blows 2006 does an excellent job outlining the challenges presented by the complex and polygenic trait of mate choice, which may commonly have complex gene action involving both epistasis and pleiotropy. Mapping female preference is challenging, but Moehring, et al. 2006 presents an elegant and rare example. Kronforst, et al. 2006 studies the joint effects of female preference and male mating traits, finding that these are affected by the same genomic region. Etges, et al. 2007 provides a rare example of mapping both male traits and fitness components, and similar studies should be more widespread. Sex chromosomes may play a special role, and both Kitano, et al. 2009 and Saether, et al. 2007 find loci on the sex chromosomes that cause premating isolation. Clustering of mating traits and ecological traits in the genome should facilitate speciation, and Malek, et al. 2012 finds evidence for such clustering. Other efforts such as Abzhanov, et al. 2004 and Abzhanov, et al. 2006 have focused on finding the actual genes and mutations that cause variation in traits that cause isolation through sexual selection.

Abzhanov, A., W. P. Kuo, C. Hartmann, B. R. Grant, P. R. Grant, and C. J. Tabin. 2006. The calmodulin pathway and evolution of elongated beak morphology in Darwin's finches. *Nature* 442:563–567.

Following up on Abzhanov, et al. 2004, this microarray study surveys genes with no previously known effect on beak development, identifying a new gene, CaM. Comparing expression levels in wild species and functional analysis shows that higher expression of CaM correlates with longer beaks. Bmp4 and CaM independently alter beak shape, and thus can evolve independently. These two studies together identify two genes simultaneously affecting adaptation, mate choice, and speciation, and demonstrate methods that can be applied in other systems.

Abzhanov, A., M. E. Protas, B. R. Grant, P. R. Grant, and C. J. Tabin. 2004. Bmp4 and morphological variation of beaks in Darwin's finches. *Science* 305:1462–1465.

Darwin's finches are iconic examples of speciation. Beak size and shape are adaptations for different diets and also influence song structure; therefore, they are keys to premating and postmating isolation. This pioneering study takes a candidate gene approach to identifying Bmp4 as one of the key genes responsible for variation among species in the depth and breadth of beaks, and this study explores how changes in Bmp4 expression throughout development affect beak shape.

Chenoweth, S. F., and M. W. Blows. 2006. Dissecting the complex genetic basis of mate choice. *Nature Reviews Genetics* 7:681–692.

This review tackles a challenging topic—the genetics of mating preferences—and argues for an integration of quantitative genetics and genomics approaches to uncover the genetic basis of mating traits, including mate choice and mating signals. Examples of how these approaches can be applied to gain insight into complex signals and choice behavior are used to illustrate how to identify the traits under sexual selection, the genetic polymorphisms that give rise to variation, and the genes that code for mating traits.

Etges, W. J., C. C. de Oliveira, E. Gragg, D. Ortiz-Barrientos, M. A. Noor, and M. G. Ritchie. 2007. Genetics of incipient speciation in *Drosophila mojavensis*. I. Male courtship song, mating success, and genotype x environment interactions. *Evolution* 61:1106–1119.

A very nice and rare example of genetically mapping a male mating trait and mating success. This study is particularly interesting in considering genotype by environment interactions caused by being raised on different cacti and these interactions are thought to be the basis of incipient speciation in this system.

Kitano, J., J. A. Ross, S. Mori, et al. 2009. A role for a neo-sex chromosome in stickleback speciation. *Nature* 461:1079–1083.

The evolution of sex chromosomes and the role that sex chromosomes play in speciation are not often considered in conjunction. This paper shows that genomic regions for sexual isolation and male sterility are located on sex chromosomes in stickleback fish and, furthermore, that the recent evolution of the sex chromosome in one species by chromosomal fusion contributes substantially to reproductive isolation. The paper is important both for identifying genomic regions contributing to speciation and for testing theoretical models of sex chromosome evolution.

Kronforst, M. R., L. G. Young, D. D. Kapan, C. McNeely, R. J. O'Neill, and L. E. Gilbert. 2006. Linkage of butterfly mate preference and wing color preference cue at the genomic location of wingless. *Proceedings of the National Academy of Sciences of the United States of America* 103:6575–6580.

This study uses genetic mapping to test for a magic trait, and finds that wing color and color preference colocalize to the same genomic region in two *Heliconius* butterflies, where color pattern is known to contribute to reproductive isolation. This is one of the early empirical genomics papers to find evidence of linkage between mate preference and the preferred trait.

Malek, T. B., J. W. Boughman, I. Dworkin, and C. L. Peichel. 2012. Admixture mapping of male nuptial colour and body shape in a recently formed hybrid population of threespine stickleback. *Molecular Ecology* 21:5265–5279.

This innovative study uses admixture mapping in naturally occurring hybrids to find genomic regions for two traits known to contribute to reproductive isolation in stickleback species pairs—color and shape.

Moehring, A. J., A. Llopart, S. Elwyn, J. A. Coyne, and T. F. C. Mackay. 2006. The genetic basis of prezygotic reproductive isolation between *Drosophila santomea* and *D. yakuba* due to mating preference. *Genetics* 173:215–223.

In one of the few studies that dissects the genetic basis of female preference in the context of speciation, a small number of quantitative trait loci are found that affect mating discrimination, only partly shared between multiple parapatric pairs of *Drosophila*. These findings suggest that independent speciation events are based on some, but not all, of the same genetic mechanisms.

Saether, S. A., G. P. Saetre, T. Borge, et al. 2007. Sex chromosome-linked species recognition and evolution of reproductive isolation in flycatchers. *Science* 318:95–97.

Assortative mating is facilitated when mating traits and/or mating preferences and other components of reproductive isolation are located on the sex chromosomes, because sex linkage reduces recombination between these traits, maintaining linkage between species recognition and hybrid unfitness. Capitalizing on the long-term data for pied and collared flycatchers, this was one of the first studies to show such sex linkage. The study also rules out imprinting as an explanation for assortative mating in these flycatchers.

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