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Behavioral Isolation and Incipient Speciation in Birds

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Abstract

Behavioral changes, such as those involved in mating, foraging, and migration, can generate reproductive barriers between populations. Birds, in particular, are known for their great diversity in these behaviors, and so behavioral isolation is often proposed to be the major driver of speciation. Here, we review empirical evidence to evaluate the importance of behavioral isolation in the early stages of avian speciation. Experimentally measured mating preferences indicate that changes in mating behavior can result in premating barriers, with their strength depending on the extent of divergence in mating signals. Differences in migratory and foraging behavior also can play important roles in generating reproductive barriers in the early stages of speciation. However, because premating behavioral isolation is imperfect, extrinsic postzygotic barriers, in the form of selection against hybrids having intermediate phenotypes, also play an important role in avian diversification, especially in completing the speciation process.

1. INTRODUCTION

Reproductive isolation defines biological species (Dobzhansky 1937, Mayr 1942). As such, the study of the origin of species is essentially the study of how barriers that prevent gene flow between divergent populations evolve (Coyne & Orr 2004). These reproductive barriers are often characterized as acting either before or after zygotes are formed (Dobzhansky 1937, Mayr 1942). Several general patterns have emerged from comparative studies in plants and animals on the evolution of these barriers, which include the observations that reproductive isolation between taxa increases with time since divergence and that the heterogametic sex is disproportionately affected by hybrid sterility and inviability (Haldane's rule), both forms of intrinsic postzygotic barriers (Coyne & Orr 1997, Presgraves 2002). Despite such generalities, taxa vary in the relative importance of pre- and postzygotic barriers as isolating mechanisms and in their relative rates of evolution. For example, in *Drosophila* and several flowering plants, prezygotic barriers evolve before hybrid sterility and inviability (Baack et al. 2015, Coyne & Orr 1997), though more subtle postzygotic barriers are less often studied. Conversely, intrinsic postzygotic barriers can evolve with little to no prezygotic isolation, as in *Tigriopus* copepods (Willett 2011). With respect to rates of evolution, prezygotic isolation in the form of pollen and ovule incompatibility evolves faster in annual than in perennial plants (Baack et al. 2015), whereas hybrid inviability evolves faster in mammals than in birds and frogs (Wilson et al. 1974). This variation in the evolution of reproductive barriers is likely mediated by taxon-specific aspects of mating systems, ecology, genetics, and geography (Mayr 1942).

In birds, which are known for their great diversity in display traits used to compete for and attract potential mates (Andersson 1994), prezygotic isolation is thought to be the major mechanism of reproductive isolation (Hinde 1959, Price 2007). This assertion is based on at least two key observations. First, early naturalists, including Darwin (1871), noted that traits associated with mate choice or male–male competition differ most among closely related taxa, inspiring the hypothesis that diversifying sexual selection is a major engine of speciation (West-Eberhard 1983). Second, many distantly related avian taxa can hybridize with little to no intrinsic genetic incompatibility (Grant & Grant 1992, Short 1969), yet many closely related species still coexist sympatrically. In fact, hybrid sterility and inviability in birds generally evolve after behavioral premating reproductive isolation is complete (Price & Bouvier 2002). Isolating mechanisms other than intrinsic postzygotic barriers therefore are likely more important as drivers of avian speciation.

Traits that result in premating isolation can evolve while populations are geographically isolated (allopatric), with natural selection, sexual selection, and/or genetic drift causing changes in preferences and corresponding display traits. Disruptive sexual selection, in particular, can drive change in mating preferences (usually in females) and corresponding display traits (usually in males), resulting in nonrandom pairing or mating between individuals of similar phenotypes [assortative mating; reviewed by Ritchie (2007)]. Moreover, diversifying natural selection can cause adaptive divergence of traits not used in mate choice, which can then be later co-opted as mating signals that facilitate assortative mating [magic traits; reviewed by Servedio et al. (2011)]. Finally, mutation and genetic drift can change display traits and preferences primarily through the loss of display elements (Kaneshiro 1980), which can be especially important in such culturally transmitted traits as bird song (Grant & Grant 1996).

Despite the focus on premating barriers as critical in avian speciation, the observations that hybridization can occur between well-established species and that hybrids are typically common in narrow zones of species contact suggest that premating reproductive barriers are imperfect and other isolating mechanisms are important (Grant & Grant 1992, Price & Bouvier 2002, Short 1969). Reproductive barriers in the form of extrinsic postzygotic isolation can arise if genetically viable hybrids of intermediate phenotype fail to attract and compete for mates or fail to find suitable ecological conditions (Coyne & Orr 2004, Price 2007). Extrinsic postzygotic isolation, in turn, may cause character displacement in signals used in mate recognition, thus reinforcing premating barriers and reducing the frequency of hybridization (reinforcement; Dobzhansky 1937). In short, by promoting assortative mating, pre- and postzygotic reproductive barriers seem to be important in avian speciation, with prezygotic barriers either evolving in complete allopatry or being reinforced when populations come into secondary contact and selection favors mechanisms to avoid hybridization.

On the basis of the decades of research on avian speciation, we review how behavioral changes, acting in concert with divergent morphological traits, can result in both pre- and postzygotic reproductive barriers despite a lack of genetic incompatibility. We include morphological traits that are used in behavioral interactions (e.g., plumage color), because selection necessary to maintain differences in these traits is likely mediated by behavior (e.g., mate choice) and therefore related to social selection within each population. We also review other mechanisms that can lead to behavioral isolation, such as differences in dispersal ability and in migratory, foraging, and flocking behaviors. Finally, we discuss the influence of sexual imprinting and learning in behavioral isolation as well as other outstanding questions on the role of behavioral isolation in incipient speciation in birds.

2. MECHANISMS FOR BEHAVIORAL ISOLATION

A variety of behaviors can contribute to reproductive isolation between populations by promoting assortative mating and/or by causing low fitness of hybrids. Behavioral mechanisms of isolation include changes in mating preferences and display traits, assortative flocking, limited dispersal, and distinct habitat preferences or migratory behavior. We discuss each of these mechanisms, as well as the interaction of behavior and morphology, in turn below.

2.1. Divergence in Secondary Sexual Traits

Coevolutionary changes in display traits and mating preferences have been proposed as major drivers of speciation in birds (Price 2007, West-Eberhard 1983). Theoretical and comparative work over the past few decades, however, provides only equivocal support for this hypothesis. Theoretical studies suggest that diversifying sexual selection, under certain conditions, can drive speciation; however, the conditions are restrictive and, more likely, both sexual and natural selection act in concert to drive divergence and cause reproductive isolation [reviewed by Servedio & Boughman (2017)]. Moreover, although some comparative studies indicate that species richness or speciation rate in birds is predicted by proxies for the intensity of sexual selection (e.g., Barraclough et al. 1995, Mason et al. 2017), other comparative analyses have found that feeding ecology or behavioral flexibility are better predictors (e.g., Huang & Rabosky 2014, Nicolakakis et al. 2003, Phillimore et al. 2006). Despite the equivocal results of comparative and theoretical work, studies comparing closely related species of birds seem to suggest that changes in mating signals and preferences may cause behavioral isolation, especially at the early stages of speciation.

2.1.1. Divergence and coevolution of male traits and female preferences. Distinct polymorphisms in reproductive traits do arise within populations (Lamichhaney et al. 2016, Tuttle et al. 2016); however, most cases of divergence resulting in speciation are initiated in allopatry (Mayr 1942, Price 2007). Most studies, therefore, explore differences between populations that are allopatric, or initially allopatric, before establishing secondary contact.

Differentiated, allopatric populations, such as distinct subspecies or incipient species, may have diverged with respect to display traits sufficiently to cause behavioral isolation when populations come into secondary contact. Experimental studies that simulate contact between allopatric populations generally indicate that females prefer signals from their own population (**Table 1**). For example, playback experiments have shown that female swamp sparrows (*Melospiza georgiana*) from the coastal subspecies preferred songs from their own population (homotypic) over songs from another population/subspecies (heterotypic), suggesting behavioral isolation between the two (Ballentine et al. 2013). Studies in which females have shown preference for homotypic over heterotypic songs and/or plumage color among allopatric taxa are summarized in **Table 1**. Interestingly, some of the studies in **Table 1** show that preferences for homotypic over heterotypic signals can evolve rapidly, even between populations that vary only in song dialects and are morphologically indistinguishable and exhibit little population genetic structure.

Cases in which allopatric populations come into secondary contact provide natural experiments to test for the presence and strength of reproductive barriers. In virtually all published studies that have quantified mating preferences (**Table 1**), differences that evolved in allopatry are maintained at secondary contact through assortative mating. For example, in cases in which two subspecies of song sparrow (*Melospiza melodia fallax* and *Melospiza melodia heermanni*) have established secondary contact in the southern Coachella Valley of California, females solicited more copulations from males with homotypic songs and plumage color than from males with heterotypic display traits (Patten et al. 2004). Similarly, in a hybrid zone between the lazuli (*Passerina amoena*) and indigo (*Passerina cyanea*) buntings, females from both species preferred males with conspecific over heterospecific plumage color and song (Baker 1991, Baker & Baker 1990). A few observational studies, however, have indicated a lack of assortative mating at contact zones. For example, observations of social pairs in two subspecies of the yellow-rumped warbler (*Setophaga coronata*) revealed a pattern consistent with random mating despite the maintenance of genetically distinct subspecies, suggesting postzygotic barriers are likely more important (Brelsford & Irwin 2009). Despite a few exceptions from field observations (**Supplemental Table 1**), a clear consensus from experimental data favors a strong preference for homotypic color or song, consistent with the hypothesis that behavioral isolation is important in maintaining distinct populations in the face of potential gene flow upon secondary contact (see **Table 1**). In fact, even genetic studies that did not directly test for mating preferences revealed a general consensus that many species boundaries are semipermeable upon secondary contact but that hybrids are kept within distinct hybrid zones, presumably due to their lower fitness [reviewed by Ottenburghs et al. (2017)].

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When selection against hybridization is strong, yet considerable heterospecific mating still occurs, assortative pairing could be enhanced through reinforcement of preference and display traits. Evidence for reinforcement is rare (Marshall et al. 2002), especially in birds. However, displacement of display traits and/or preferences has been observed when isolated populations come into secondary contact (Kirschel et al. 2009, Seddon & Tobias 2010). In the hybrid zone between the closely related white-collared (*Ficedula albicollis*) and pied (*Ficedula hypoleuca*) flycatchers, for instance, hybrid females are sterile and hybrid males suffer a mating disadvantage, as they are less attractive to females (Svedin et al. 2008). Plumage differences are exaggerated in the hybrid zone, apparently a result of selection for conspecific recognition and against heterospecific pairing (Sætre et al. 1997). When heterospecific pairings do occur, they are caused primarily by a lack of potential conspecific mates. However, females can reduce the incidence of hybridization by soliciting extrapair matings from conspecifics or by preferentially fertilizing eggs with conspecific sperm through cryptic choice and sperm competition (Cramer et al. 2016).

Other studies provide evidence consistent with reproductive character displacement in birds, as there often seems to be enhanced recognition of conspecifics by territorial males in regions of

Table 1 Experimental studies exploring mating preferences for homotypic and heterotypic signals

Comparison (taxon pair)	Basis of reproductive isolation	Methods*	Assay**	Geography	Traits for species-specific male aggression	Sexes use the same signals for species recognition	Greater species discrimination in sympatry?	Reference(s)
Snow goose (*Anser caerulescens*) Color morphs	Plumage color	FO, AV	AP	Allopatric with contact zone; study at contact zone	Unknown/not tested	Not tested	Not tested	Cooke et al. 1976
California quail (*Callipepla californica*) Gambel's quail (*Callipepla gambelii*)	Preferred conspecific but basis of choice unknown	LE	CS, AT	Allopatric with hybrid zone; study at hybrid zone	Unknown/not tested	Not tested	No	Gee 2003
Brown booby (*Sula leucogaster*) Color morphs	Plumage color	FE	AP, NC	Allopatric with contact zone; study near and away from contact zone	Unknown/not tested	Not tested	Yes	López-Rull et al. 2016
Peruvian warbling antbird (*Hypocnemis peruviana*) Yellow-breasted warbling antbird (*Hypocnemis subflava*)	Song	FE, PE	SR	Allopatric with sympatric zone; studies at sympatric zones	Song	Yes	Not tested (but males were tested for aggressive response)	Seddon & Tobias 2010, Tobias & Seddon 2009
Red-backed fairywren (*Malurus melanocephalus cruentatus* and *Malurus melanocephalus melanocephalus*)	Plumage color (but asymmetrical preference for red subspecies; song not tested)	FE	EPM	Allopatric with hybrid zone; study at hybrid zone	Song (response to homo- and heterotypic plumage is similar)	No	No	Baldassarre & Webster 2013, Greig et al. 2015
Barn swallow (*Hirundo rustica transitiva*, *Hirundo rustica savignii*, and *Hirundo rustica rustica*)	Plumage color and tail length	FE	EPM	Allopatric	Unknown/not tested	Not tested	Not applicable	Vortman et al. 2013
Barn swallow (*Hirundo rustica transitiva*, *Hirundo rustica rustica*, and *Hirundo rustica erythrogaster*)	Plumage color and tail length	FE	EPM	Allopatric	Unknown/not tested	Not tested	Not applicable	Safran et al. 2016
Black-crested titmouse (*Baeolophus atricristatus*) Tufted titmouse (*Baeolophus bicolor*)	Song and (weakly) plumage	FE, LE	AT	Allopatric with hybrid zone; study at hybrid zone	Song (plumage not tested)	Yes	Not tested	Curry & Patten 2016
Pied flycatcher (*Ficedula hypoleuca*) Collared flycatcher (*Ficedula albicollis*)	Plumage color and song; timing of breeding; reduced hybrid fitness via sexual selection; female hybrid sterility	FO, AV, PE	AP, N, EPM	Allopatric with hybrid zone	Song (plumage not tested)	Yes	Yes	Qvarnström et al. 2006, Sætre & Saether 2010, Sætre et al. 1997, Veen et al. 2001

(*Continued*)

Table 1 ***(Continued)***

Comparison (taxon pair)	Basis of reproductive isolation	Methods*	Assay**	Geography	Traits for species-specific male aggression	Sexes use the same signals for species recognition	Greater species discrimination in sympatry?	Reference(s)
African stonechat (*Saxicola torquatus*) populations (90 to 180 km apart)	Song and plumage color	FE	LA	Allopatric	Song and plumage color	Yes	Not applicable	Mortega et al. 2014
Brood parasitic indigobird *Vidua* spp. with different hosts	Song	AV, FO	AT	Sympatric	Song	Yes	Not applicable	Payne et al. 1998, Sorenson et al. 2003
Zebra finch (*Taeniopygia guttata guttata* and *Taeniopygia guttata castanotis*)	Song and plumage color	LE, AV	CS, OS, AT	Allopatric	Unknown/not tested	Not tested	Not applicable	Clayton 1990
Gouldian finch (*Erythrura gouldiae*) Color morphs	Plumage color and hybrid inviability	FO, LE, MC	AP	Sympatric	Plumage color	Yes	Not applicable	Pryke & Griffith 2007, 2009
House finch (*Carpodacus mexicanus*) Color morphs	None	LE	AT	Allopatric	Unknown/not tested	Not tested	Not applicable	Hill 1994
Red crossbill (*Loxia curvirostra*) Bill morphs	Flight calls	AV	AT	Sympatric	Unknown/not tested	Not tested	Not applicable	Snowberg & Benkman 2007
Yellowhammer (*Emberiza citrinella*) Natal versus foreign dialects	Song	LE	CS, OS	Allopatric	Unknown; response to homo- and heterotypic song is similar	No	Not applicable	Baker et al. 1987a, Tietze et al. 2012
Song sparrow (*Melospiza melodia*) Pennsylvania and New York, United States, populations	Song	LE	CS, OS	Allopatric	Song	Yes	Not applicable	Searcy et al. 1997
Song sparrow (*Melospiza melodia heermanni* and *Melospiza melodia fallax*)	Song and plumage color	LE	CS, OS	Allopatric with hybrid zone; study at hybrid zone	Song (plumage color not tested)	Yes	Not tested	Patten et al. 2004
Swamp sparrow (*Melospiza georgiana*) New York and Minnesota, United States, populations/dialects	Song	LE, FE	CS, OS	Allopatric	Song (but more aggressive to heterotypic song)	No	Not applicable	Balaban 1988

(*Continued*)

Table 1 *(Continued)*

Comparison (taxon pair)	Basis of reproductive isolation	Methods*	Assay**	Geography	Traits for species-specific male aggression	Sexes use the same signals for species recognition	Greater species discrimination in sympatry?	Reference(s)
Swamp sparrow (*Melospiza georgiana georgiana*) Coastal swamp sparrow (*Melospiza georgiana nigrescens*)	Song	LE	CS, OS	Allopatric	Song	Yes	Not applicable	Ballentine et al. 2008, 2013
Rufous-collared sparrow (*Zonotrichia capensis*) populations (25 km apart)	Song	AV	CS, OS	Allopatric	Unknown; response to homo- and heterotypic song is similar	No	Not applicable	Danner et al. 2011
Puget Sound white-crowned sparrow (*Zonotrichia leucophrys pugetensis*) Conspecific versus song sparrow	Song	PE	AT, SR	Allopatric	Song	Yes	Not applicable	Nelson & Soha 2004
Nuttall's white-crowned sparrow (*Zonotrichia leucophrys nuttalli*) Natal versus foreign dialects	Song	LE	CS, OS	Allopatric	Unknown/not tested	Not tested	Not applicable	Baker 1983, Baker et al. 1987b
Red-winged blackbird (*Agelaius phoeniceus*) California and Pennsylvania, United States, populations (song)	Song and plumage (epaulets)	FE	CS, OS	Allopatric	Song and plumage (epaulets)	Yes	Not applicable	Searcy 1990, Smith 1972, Yasukawa et al. 2009
Brown-headed cowbird (*Molothrus ater ater* and *Molothrus ater obscurus*)	Song	LE	CS, OS	Allopatric	Unknown/not tested	Not tested	Not applicable	King et al. 1980
Lazuli bunting (*Passerina amoena*) Indigo bunting (*Passerina cyanea*)	Song and plumage color	AV	CS, OS	Allopatric with hybrid zone; study from allopatric sites	Song (plumage not tested)	Yes	Not tested (but male response less discriminating at hybrid zone)	Baker 1991, Baker & Baker 1990
Medium ground finch (*Geospiza fortis*) Cactus finch (*Geospiza scandens*)	Beak/body size (male mate choice)	PE	AT, COP	Allopatric and sympatric	Song and beak/body size (male and female aggression)	Yes	Yes	Ratcliffe & Grant 1983

[*] AV, aviary mate choice trials; FE, field experiments; FO, field observations; LE, laboratory experiments; MC, mating crosses; PE, playback experiments in the field.

[**] AP, assortative pairing; AT, association time; COP, copulation; CS, copulation solicitation; EPM, extra pair mating; LA, latency to approach stimuli; N, nesting; NC, number of copulations; OS, estradiol implant; SR, song response.

sympatry over those in allopatry [reviewed by Irwin & Price (1999)]. However, the few cases listed in **Table 1** that directly measured mating preferences provide little evidence of enhanced preference for conspecifics at contact zones, suggesting lack of reinforcement. One reason reinforcement may not be observed in contact/hybrid zones is that many are essentially tension zones, with net gene flow into the zone that could swamp selection within it (Barton & Hewitt 1985). In sum, in spite of a likely publication bias for positive results, behavioral isolation through divergence in male display and female preference may be common in the early stages of speciation. Accordingly, behavioral isolation would appear to evolve rapidly, even between populations with little genetic and morphological divergence (see **Table 1**).

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2.1.2. Intrasexual competition and behavioral isolation. Because territorial males respond readily to test stimuli, most field studies testing the role of divergent display traits in species recognition focus on aggressive reactions of males (rather than females) to homotypic versus heterotypic signals. A literature search for field experiments published between 1987 and 2017, using "song playback" and "species recognition" as key words, indicated that in 36 of 49 studies (73%) males preferentially responded to homotypic over heterotypic signals. Six studies found asymmetrical responses, wherein one species of the tested taxon pair preferentially responded to playbacks of homotypic songs, but the other species responded to both song types equally. The remaining 7 studies found no difference in response to homotypic versus heterotypic songs. This survey indicates general support for the hypothesis that divergent signals function in species recognition, at least for males interacting with potential competitors (**Supplemental Table 2**). However, the literature is likely biased toward publishing positive results, and so this conclusion should be accepted cautiously. One study presented results from playback experiments involving 72 pairs of related, allopatric neotropical passerines and quantified the difference in song structure between taxon pairs (Freeman & Montgomery 2017). As this was a single study, it does not suffer from publication bias. The results revealed significant variation across species in how territorial males responded to homotypic and heterotypic songs, with some species ignoring heterotypic signals and others responding equally to both song types. Importantly, the magnitude of the difference in song structure between the paired taxa predicted the likelihood that males discriminated between homo- and heterotypic song types, independent of genetic divergence (Freeman & Montgomery 2017). Overall, the positive association between signal divergence and species discrimination indicates a critical role for changes in mating signal in generating behavioral isolation (see also Sosa-Lopez et al. 2016, Tobias & Seddon 2009).

To relate the results of these playback experiments using territorial males more directly to the evolution of assortative mating, the signals used to recognize sexual competitors (typically among males) are assumed to be the same signals used in mate choice (typically by females) (e.g., Freeman & Montgomery 2017). A test of this critical assumption requires experiments that measure species recognition in both males and females, but these experiments are few. A literature review produced 17 studies in which responses to the same homotypic and heterotypic signals were tested experimentally in both males and females (**Table 1**). Thirteen of the 17 studies (76%) revealed that both sexes used the same signals for mate choice and agonistic interactions (**Table 1**), suggesting that playback experiments with aggressive males could indeed serve as an index of behavioral isolation. For example, in the song sparrow study and the lazuli/indigo bunting study discussed in Section 2.1.1, differences in song mediated species recognition in both females and males (Baker 1991, Baker & Baker 1990, Patten et al. 2004). Four of the 17 studies (24%) found, however, that males and females responded differently to the same signals. In one case, females preferred homotypic over heterotypic songs, but males surprisingly responded more aggressively to heterotypic songs (Balaban 1988). The remaining three cases found females using song or plumage to recognize potential mates, with males initiating agonistic interactions in response to any signal (**Table 1**). For instance, female rufous-collared sparrows (*Zonotrichia capensis*) preferred homotypic over heterotypic songs, but males responded aggressively to all songs regardless of origin. Similarly, in red-backed fairywrens (*Malurus melanocephalus*), manipulation of plumage to mimic another subspecies resulted in females producing young sired by extra-paired males with heterotypic plumage. Males, in contrast, attacked taxidermic mounts of either subspecies' plumage color (Baldassarre & Webster 2013, Greig et al. 2015). The more general response by aggressive males suggests that males are less discriminating than females, a pattern found in other nonavian species (Bernal et al. 2007). In fact, in no case were males more discriminating than females, which suggests that male aggressive response to playbacks may be a conservative index of conspecific recognition (see Irwin & Price 1999). However, very few studies have assessed both male and female responses, and additional work is needed to robustly test the assumption that agonistic and mating interactions are mediated by the same signals.

Although discussed decades ago (West-Eberhard 1983), the hypothesis that intrasexual competition can be a driver of speciation has only recently gained widespread attention. Largely inspired by cases in fish (e.g., Lackey & Boughman 2013), this hypothesis posits that diversifying sexual selection through intrasexual competition can drive changes in male display traits in the absence of divergence in mating preferences. In cases in which male display traits mediate the ability to control resources necessary for breeding, variation in display traits would lead to variation in reproductive success that could, in turn, lead to premating barriers. This mechanism could apply to birds, as males are often highly aggressive and defend territories or display arenas necessary for breeding (Andersson 1994). As such, the results of playback experiments discussed above could be interpreted under this hypothesis, especially in studies with controls that differentiated responses between ecological and sexual competitors.

In some cases, differences in the degree of aggression among males of different species do not produce assortative mating at secondary contact but rather one species competitively excluding the other or the asymmetrical introgression of an adaptive trait across the hybrid zone (Ottenburghs et al. 2017). For example, the Townsend's (*Setophaga townsendi*) and hermit (*Setophaga occidentalis*) warblers hybridize where their ranges overlap in western North America, and the more aggressive Townsend's warbler is replacing the hermit warbler in habitats where both species defend breeding territories (Pearson & Rohwer 2000). The result is a moving hybrid zone. These examples demonstrate the important role of intrasexual competition in determining the dynamics of hybrid zones, which, in turn, influence the outcome and completion of speciation.

2.1.3. Hybridization, postzygotic isolation, and speciation. Overall, premating isolation clearly is important in incipient speciation; however, divergent taxa of birds occasionally do hybridize, indicating that premating isolation is imperfect. In such situations, populations blend together in the absence of postzygotic isolation. Given that intrinsic postzygotic isolation evolves slowly in birds, extrinsic postzygotic barriers are likely important in promoting and maintaining species boundaries (Price 2007). For example, extrinsic postzygotic isolation can occur when hybrid males possess display traits that are intermediate and thus unattractive to either parental species (e.g., Svedin et al. 2008). Alternatively, hybrids exhibiting intermediate behavior and morphology could be less efficient in foraging or other ecological tasks than the parental phenotypes (Grant & Grant 2007; see Sections 2.3–2.5 below).

Historically, hybridization has been viewed as a force that primarily hinders speciation (Mayr 1942) by preventing differentiation and/or by causing genetic swamping and extinction of genetically unique lineages (e.g., Kleindorfer et al. 2014). However, hybridization can also be a creative process. For example, hybridization can serve as a conduit for the introgression of adaptive traits between species, which can facilitate adaptive evolution [reviewed by Ottenburghs et al. (2017)]. This introgression includes traits that are adaptive for behavioral interactions, such as song and plumage color.

Finally and more directly, hybridization can create new species when two distinct species hybridize and form a third lineage that is reproductively isolated from either parental species. Though common in plants, hybrid species have been confirmed only recently in birds. For example, genomic analyses indicate that the golden-crowned manakin (*Lepidothrix vilasboasi*) of Amazonia is a result of a hybridization event that occurred more than 100,000 years ago between the snow-capped (*Lepidothrix nattereri*) and opal-crowned (*Lepidothrix iris*) manakins (Barrera-Guzmán et al. 2017). Two other examples of hybrid species in birds include the Italian sparrow (*Passer italiae*), which originated from hybridization between the house (*Passer domesticus*) and Spanish (*Passer hispaniolensis*) sparrows approximately 10,000 years ago (Elgvin et al. 2017), and a putative new hybrid species of Darwin's finch on Daphne Major island in the Galápagos Islands, which was established within a few generations, initiated by a breeding event between an immigrant large cactus finch (*Geospiza conirostris*) and a resident medium ground finch (*Geospiza fortis*) (Lamichhaney et al. 2017). In all three cases of hybrid speciation, behavioral barriers seem critical in maintaining species boundaries in sympatry, as the hybrid species possess mating signals that are intermediate or distinct from those of the parental species. Given low genetic incompatibilities between well-established species (Grant & Grant 1992) and the advent of new sequencing technology, it would not be surprising if other examples of hybrid avian species are found in the next few years.

2.2. Assortative Flocking or Grouping

Assortative mating leading to reproductive isolation might also arise, even in sympatry, from ecological specialization that leads to spatial groupings of phenotypically similar individuals. Perhaps the best-studied case in birds is that of the red crossbill (*Loxia curvirostra*) complex. In crossbills, disruptive ecological selection has led to several subpopulations that differ in bill morphology, each adapted to foraging on seeds from a particular conifer species (Benkman 2003). These subpopulations are referred to as call types because they also differ in the vocalizations used to coordinate movements in foraging flocks (Groth 1993). In this system, three interrelated mechanisms appear to produce assortative mating by call type. First, call type subpopulations tend to be spatially segregated in at least some parts of their range, because the tree species on which each specializes do not fully co-occur (Smith & Benkman 2007). Second, even in areas where they do co-occur, birds of the same call type typically flock together; individual birds are more strongly attracted to calls of their own call type than to other call types, likely because calls are a form of public information for finding suitable food resources (Smith et al. 2012). Because mate selection tends to occur within foraging flocks, assortative flocking produces assortative mating as a by-product. Finally, even in the absence of co-flocking, females tend to choose males of their own call type on the basis of vocal signals (Snowberg & Benkman 2007). In this case, female preference for males of the same song type is likely favored by production of offspring that are well adapted for foraging (Snowberg & Benkman 2007). Thus, in this system, multiple mechanisms appear to favor assortative associations among similar birds, facilitating behavioral isolation across call types and adaptive divergence.

Assortative grouping, leading to assortative mating and reproductive isolation, may occur in other taxa as well, including other cardueline finches (e.g., Badyaev et al. 2008) and species in which foraging efficiency favors morphological specialization. For example, island scrub jays (*Aphelocoma insularis*) in pine stands have narrower, longer bills than do those in oak habitats, likely due to selection for foraging adaptations in the two habitat types (Langin et al. 2015). The population exhibits positive assortative mating by bill size, which appears to have led to subtle, yet significant, genetic differences between jays across habitat types (Langin et al. 2015). However, it is not clear whether this pattern has arisen because habitat preferences affect mating patterns directly or because bill size affects vocalizations that might be involved in pair formation (Langin et al. 2017; see Section 3 below).

2.3. Limited Dispersal

Reproductive isolation might also arise from limited dispersal ability, even without significant ecological differences between regions. If geographic barriers to dispersal were semipermeable—that is, if dispersal across a barrier is possible but difficult—then rare dispersal events would lead to colonization of new regions with limited gene flow between the parent and daughter populations (Price 2007). Reduced gene flow would allow for divergence in sexual signals or other traits even without strong selection for local ecological adaptation.

Dispersal ability is an important driver of diversification in at least some regions and/or groups of birds. For example, one large-scale comparative study (Smith et al. 2014) has shown that much of the diversification of neotropical lowland birds has occurred after major geologic events and is best explained by lineage age and ecological factors that affect dispersal ability. Specifically, older lineages (which have had more time to colonize new areas) and those with limited dispersal ability (e.g., understory versus canopy species) showed higher rates of phylogeographic diversification. Similarly, species with morphologies (i.e., wing shape) associated with high dispersal ability show reduced levels of phylogeographic differentiation compared to those with low dispersal ability (Claramunt et al. 2012; but see Kennedy et al. 2016).

2.4. Seasonal Migration and Migratory Divides

Most bird speciation research has focused on the breeding season, because that is when reproductive isolation most obviously manifests itself; however, variation in behavior outside the breeding season, including seasonal migratory behavior, can cause reproductive isolation [reviewed by Turbek et al. (2017)].

Prezygotic isolation can result from different timing of spring migration, such that individuals wintering in different areas arrive on the breeding grounds and pair at different times (e.g., Bearhop et al. 2005). Prezygotic isolation could also arise more indirectly as a result of migratory differences, if different migratory behaviors lead to different morphologies or display traits, producing assortative mating based on those traits (Rolshausen et al. 2009).

Extrinsic postzygotic isolation, in which hybrids have lower fitness, might result from migratory differences (Turbek et al. 2017). This possibility has been investigated mostly in the context of migratory divides, narrow contact zones between two populations with divergent migratory routes (Bensch et al. 2002, Delmore & Irwin 2014, Helbig 1996, Irwin & Irwin 2005, Ruegg & Smith 2002). Often, the two routes skirt opposite sides of a region that is difficult to cross, because of a lack of refueling opportunities or difficult flying conditions (e.g., mountains, open water, or desert without opportunity for rest). For example, Eurasian blackcap warblers (*Sylvia atricapilla*) use two major migratory routes: one from western Europe southwest to Spain and then south to West Africa, and the other from eastern Europe southeast to the Middle East and then East Africa. The region between these routes contains areas that are more difficult to migrate across. Other examples occur in north–central Asia [e.g., western and eastern Siberian forms of greenish warblers, *Phylloscopus trochiloides viridanus* and *Phylloscopus trochiloides plumbeitarsus* (Irwin & Irwin

2005)] and in North America [e.g., west coast and inland forms of Swainson's thrush, *Catharus ustulatus ustulatus* and *Catharus ustulatus swainsoni* (Delmore et al. 2016, Ruegg & Smith 2002)].

A variety of studies have built support for the idea that the migratory route is largely genetically determined in many species (see Delmore & Liedvogel 2016), such that hybrids may have intermediate or mixed routes and associated traits. For instance, laboratory-reared hybrids between southwest- and southeast-orienting parental populations of blackcap warblers tended to orient directly southward, a direction that would bring them down the central, presumably inferior route (Helbig 1996). Similarly, Swainson's thrush populations on either side of a hybrid zone in western Canada take well-separated west coast and eastern North American routes to their wintering grounds in Central and South America, whereas birds of various hybrid genotypes tend to have intermediate or mixed routes (Delmore & Irwin 2014).

Broad literature surveys also point to associations between specific/subspecific designations (a proxy for reproductive isolation) and differentiated migratory behaviors (Delmore et al. 2015, Irwin & Irwin 2005). Molt scheduling provides an example of how migratory behavior can interact with morphological and physiological traits (Rohwer & Irwin 2011). For instance, in a number of North American pairs of western and eastern taxa, the western form undergoes postbreeding molting after migrating southward, whereas the eastern form molts on the breeding grounds, before migration. In at least one case, a hybrid between western and eastern forms apparently underwent two postbreeding molts, one before and one after migration, likely a suboptimal behavior because of unnecessary expenditure of time and energy (Rohwer & Irwin 2011).

In many narrow hybrid zones that correspond to migratory divides, little if any assortative mating occurs aside from that caused by spatial segregation of the distinct phenotypes; however, genetic and/or phenotypic patterns indicate that selection maintains the narrow hybrid zone [e.g., willow warblers, *Phylloscopus trochilus* (Liedvogel et al. 2014); yellow-rumped warblers, *Setophaga coronata auduboni* and *Setophaga coronata* (Brelsford & Irwin 2009); and European barn swallows, *Hirundo rustica rustica* (von Rönn et al. 2016)]. Such observations suggest that migratory differences could select against hybrids at the very early stages of speciation, before other forms of isolation develop. However, although substantial evidence shows that hybrids have mixed migratory behavior and there are compelling reasons to think that mixed behavior would be inferior, no study has yet directly determined whether hybrids have lower fitness as a result of their migratory behavior. This is partly due to limitations of current tracking devices. For example, light-level geolocators usually need to be recovered from an individual before route data can be downloaded, meaning that routes of birds that die during migration are not perceived. Advances in tracking technology and/or studies on larger species (which can carry currently available satellite tracking devices) may allow a more direct test of whether hybrids have lower fitness due to suboptimal migratory behavior.

2.5. Interaction Between Behavior and Morphology

Behavioral mechanisms that affect reproductive isolation can lead to divergence in morphological traits, as seen in the case of reproductive character displacement in *Ficedula* flycatchers discussed in Section 2.1.1. In the current section, we discuss the interaction between behavior and morphological traits not initially linked to mate choice or other social interactions, such as so-called magic traits that affect both ecological differentiation and reproductive isolation between populations. Mounting evidence suggests that such traits might be common in at least some taxa, though this remains uncertain (Servedio et al. 2011). In birds, the few cases that have been suggested involve the diversification of bill size by ecological selection, which, in turn, may affect the production and qualities of mating signals. For example, closely related species of Darwin's finches (*Geospiza* spp.)

differ in bill size and shape due to selection by their ability to exploit different food resources (Grant & Grant 2007). These bill size differences are, in turn, biomechanically associated with differences in male song (Podos 2001), which is important for pair formation and territorial defense (Grant & Grant 2007). In these cases, though, it is unclear whether changes in song and behavioral isolation have arisen as incidental by-products of changes in bill size/shape or whether selection has directly favored changes in song to reduce hybridization. In crossbills, in which foraging demands have driven changes in bill size (Benkman 2003), acoustic differences in calls between subpopulations were not related to differences in bill size, suggesting that call types have diversified in part because of the benefits of assortative flocking (Smith et al. 2012). Other examples in which selection for increased foraging efficiency is thought to have led to differentiation in bill size/shape, and thus acoustic signals, include other finches (Badyaev et al. 2008), sparrows (Ballentine et al. 2013), and possibly island scrub jays (Langin et al. 2017).

3. LEARNING AND IMPRINTING

Because the mode of signal transmission should affect the evolution of assortative mating and the efficacy of other isolating mechanisms (Verzijden et al. 2012), we ask whether behavioral isolation is genetically determined, learned, or both. In birds, both learning and genetics play key roles in the development of behaviors as diverse as singing and mating preferences, foraging and habitat preferences, and migration patterns (Slagsvold & Wiebe 2011). Any of these might potentially affect reproductive isolation between populations. Considerable attention has been paid to the role of learning in both the development of sexual signals (e.g., birdsong) and the response to those signals (i.e., preferences). Because these (potentially) learned behaviors directly affect reproduction, they are important in behavioral isolation. In this section, we focus most of our attention on these behaviors.

Learning plays a key role in the development of song in at least three groups of birds: the oscine passerines, parrots, and hummingbirds (Baptista & Schuchmann 1990, Nottebohm 1972). Moreover, mounting evidence suggests that learning is also important for at least some species in avian clades that are traditionally thought to have songs that are largely innate, such as some suboscine passerines (Kroodsma et al. 2013). One key consequence of song learning is that it can lead to rapid cultural evolution (Mason et al. 2017), which facilitates the divergence of signals across populations by creating regional dialects (Mundinger 1982; see **Table 1**). As discussed above, both male and female birds react more strongly to local over foreign song dialects, which would facilitate behavioral reproductive isolation between populations (Section 2.1 and **Table 1**).

Although learned signals, including song, can lead to behavioral isolation between populations, this isolation can be weak or even absent despite song differences across populations (Kenyon et al. 2017, McEntee et al. 2016). This lack of reproductive isolation is likely a consequence of song learning itself, which can be flexible or even open-ended in many species. For example, if adult males could learn new songs, it could facilitate their ability to reproduce in newly adopted populations. Likewise, the male offspring of immigrant females would learn the local dialect, leading to gene flow and introgression of other (nonsong) traits despite song differences (Greig & Webster 2013). Similarly, in zones of contact between populations that have diverged in song, learning can facilitate the ability of males in each population to learn and use each other's songs, such that song differences across individuals are decoupled from genetic differences (Kenyon et al. 2017, McEntee et al. 2016, Secondi et al. 2003). These effects may explain why song discrimination and the isolating effects of song are often weaker in areas of sympatry than in allopatry (Lipshutz et al. 2017).

Just as sexual signals, particularly song, may be learned, so too may be the responses to those signals. For example, when cross-fostered birds from two different subspecies of zebra finch (*Taeniopygia guttata*) were allowed to choose mates freely, birds raised by adults of their own subspecies tended to pair assortatively with others of their own subspecies, whereas birds raised by adults of a different subspecies chose individuals of the subspecies that raised them (Clayton 1990). This process of sexual imprinting—in which young birds learn traits that affect their mating decisions later in life—has been well studied in birds [reviewed by Irwin & Price (1999)]. The most basic outcome of sexual imprinting is assortative mating, and it is easy to see that this can lead to reproductive isolation in which populations differ in key phenotypic traits. Indeed, imprinting has been found to have strong effects on mating patterns in several species of birds under natural or seminatural conditions (Cooke & McNally 1975, Warriner et al. 1963). Good examples are provided by brood-parasitic *Vidua* indigobirds, for which imprinting on host songs by both males and females appears to facilitate assortative mating and create behavioral isolation among populations specialized on different hosts (Payne et al. 2000).

Although imprinting often reinforces behavioral isolation, it also can erode isolation and facilitate gene flow across subpopulations under some conditions. First, natural cross-fostering sometimes occurs—for example, when a breeding pair takes over the active nesting site of another species (Rowley & Chapman 1986) or when a facultative brood parasite lays an egg in the nest of a different species (Lyon & Eadie 1991). In these situations, imprinting on the wrong host species may cause birds to develop mating preferences for heterospecifics, leading to hybridization and gene flow (Slagsvold et al. 2002, Sorenson et al. 2010). However, hybrid pairings as a result of imprinting appear to be rare in species with facultative brood parasitism, possibly because other mechanisms facilitate conspecific pairing (Sorenson et al. 2010). Indeed, in species that interact little with conspecifics early in life, early life experiences appear to have little effect on species recognition or pairing patterns later in life (Hauber et al. 2001, King & West 1977).

The second way that imprinting can lead to a breakdown of behavioral isolation occurs when potentially hybridizing species have similar sexual signals and/or imprinting syndromes, as would likely occur in the early stages of population divergence. In these cases, the generalized rules learned during imprinting for recognizing suitable mates might not exclude closely related populations with similar mating signals (Irwin & Price 1999). For example, hybridization in Darwin's finches (*Geospiza* spp.) is most common when parental species have similar morphology and/or songs (Grant & Grant 1997). Again, in cases in which both species occur together and hybridization is costly, we would expect selection to favor more restricted imprinting, such that recognition rules are not overly generalized or too permissive; selection might also favor genetic assimilation, such that mating preferences are inherited genetically with reduced reliance on learning (see Irwin & Price 1999).

More recent work suggests more complex interactions between learning and genetic mechanisms. For instance, returning to the pied flycatcher and white-collared flycatcher example, cross-fostering experiments indicate that young birds more actively respond to conspecific songs, even though they were raised by heterospecifics. Furthermore, the song response of hybrid nestlings does not depend on their social experience or the maternal species (Wheatcroft & Qvarnström 2017). These results suggest that early song discrimination by immature birds has a genetic basis. Similar results have been found in other songbirds, in which songs are learned by immature males during the sensitive phase of memorization but individuals have a genetic predisposition to learn conspecific songs (Catchpole & Slater 2003).

4. GENETIC BASIS OF BEHAVIORAL ISOLATION

Recent advances in DNA sequencing technology, bioinformatics, and evolutionary theory have produced a rapid increase in our understanding of the genetic differences between species [reviewed by Toews et al. (2016a)]. By incorporating studies of behavioral variation, biologists are developing an understanding of the genetic basis of behavioral isolation.

4.1. Divergence Needed in Only a Small Part of the Genome

For most of the twentieth century, speciation was usually viewed as a phenomenon in which most of the genome became differentiated between populations. A major shift in thinking occurred toward the end of the century (e.g., Wu 2001), with increasing realization that speciation can occur as a result of differentiation of only a small part of the genome. Moreover, substantial gene flow can occur during the early and middle phases of speciation, homogenizing much of the genome. Since then, genome sequencing has strengthened that view, providing many examples in which taxa long recognized as distinct species are differentiated in only a few small regions of the genome, against a background of general homogeneity (Ravinet et al. 2017).

Extreme examples of this pattern are seen in golden-winged and blue-winged warblers (*Vermivora chrysoptera* and *Vermivora cyanoptera*), which differ in only six small regions of the genome (Toews et al. 2016b); in the chestnut-bellied and melanic subspecies of the monarch flycatcher (*Monarcha castaneiventris megarhynchus* and *Monarcha castaneiventris ugiensis*), in which only a single point mutation in the *melanocortin-1 receptor* gene distinguishes the two color forms (Cooper & Uy 2017, Uy et al. 2016); and in carrion and hooded crows (*Corvus corone* and *Corvus corone cornix*), in which only 0.28% of the genome clearly separates the two species (Poelstra et al. 2014). Extensive hybridization occurs between each of these taxon pairs, such that much of the genome can flow between taxa. The highly differentiated regions contain genes known to have roles in plumage color, which in each case differs noticeably between species and forms. Divergent plumage color, in turn, likely mediates species recognition and behavioral isolation (e.g., **Table 1**).

4.2. Genomic Architecture and Evolvability

We now turn to the genomic architecture of behavioral traits themselves. Behavioral traits are more difficult to quantify than are plumage color traits, and hence less is known about their genetic bases. However, one area of substantial progress centers on migratory behavior. Migratory restlessness (Berthold & Querner 1981) and orientation (e.g., Helbig 1996) of blackcap warblers have a strong genetic basis and are remarkably evolvable. In laboratory breeding experiments between southwest- and southeast-migrating blackcaps, F2 hybrids showed much more variation in migratory orientation than F1 hybrids, suggesting a role for a small number of genes of major effect (rather than many genes of small effect) (Helbig 1996).

Bensch et al. (2002) surveyed thousands of markers and identified a single nucleotide polymorphism (SNP) that differed strongly in allele frequency between southern and northern subspecies of willow warblers in Scandinavia. These subspecies are separated by a migratory divide similar to that of the blackcap warblers, with the southern willow warblers wintering in West Africa and the northern willow warblers wintering in East Africa. More recent analyses using larger numbers of SNPs (Liedvogel et al. 2014, Lundberg et al. 2017) found little differentiation across most of the genome, with just 3 blocks of high differentiation containing 146, 135, and 53 genes, respectively, on chromosomes 1, 3, and 5. Although one of these blocks [on chromosome 3; including the locus first identified by Bensch et al. (2002)] is associated more with altitude and latitude than with migratory phenotype, the other two blocks are highly associated with geographic variation in migratory phenotype. Given that premating isolation in the migratory divide is weak, genes influencing migratory behavior could plausibly occur in these genomic clusters, and hybrids could plausibly suffer lower fitness because of suboptimal combinations of alleles, and the behaviors they confer, in these two genomic blocks.

Sampling in the Swainson's thrush migratory divide has provided a direct examination of which parts of the genome are associated with migratory route and wintering location in free-flying birds breeding within the hybrid zone. Delmore et al. (2016) identified a large (approximately 30 million base pairs) region on chromosome 4 within which allelic variation is highly associated with migratory route and wintering longitude. This region contains the circadian rhythm gene *CLOCK* (circadian rhythm is thought to play a role in migration; Delmore & Liedvogel 2016). However, the large size of this region and its physical linkage means that the particular genes responsible for migratory differences are difficult to determine with confidence. A strong possibility is that multiple closely linked loci are differentially adapted to the two migratory routes. It should be noted that this large block is only one of many regions of high differentiation between the two forms of Swainson's thrushes, suggesting the role of other traits in speciation in addition to migration.

The genomic regions associated with migratory routes differ between willow warblers (located on chromosomes 1 and 5) and Swainson's thrushes (chromosome 4), suggesting that the genetic architecture of migratory route differs among bird species. The unifying pattern in these two cases consists of loci of large effect, found in large linkage blocks that display substantial differentiation between subspecies.

Another behavior that can differ strongly between bird species is song, and recent progress has been made in understanding its genetic basis. Although learning plays a substantial role in singing behavior, it is well established that genetic differences between species influence which songs are learned (Catchpole & Slater 2003), such that song evolution can be considered an example of gene-culture evolution (Feldman & Laland 1996). Analyses of the zebra finch genome and gene expression patterns have shown that approximately 10% of the genes are regulated by singing behavior (Warren et al. 2010, Whitney et al. 2014), and much is now known about the neural circuitry involved in song learning and production [reviewed by Brainard & Doupe (2013)]. Although many genes are clearly involved in singing, less is known about the genetic architecture of differences in singing behavior between species. Nonetheless, remarkable progress in this area has been made using different strains of domesticated canaries (*Serinus canaria*) (Mundinger & Lahti 2014). By producing hybrids and backcrosses via captive breeding and by rearing offspring in acoustic isolation chambers with controlled exposure to songs of the two strains, Mundinger & Lahti (2014) showed a strong effect of both autosomes and the Z chromosome (a sex chromosome) in determining which songs were learned, mostly in an additive manner.

Aside from migratory and singing behavior, the genetic architecture of other behavioral differences between bird species has received little attention. However, within-population analyses of variation in social and mate-choice behaviors show strong potential for loci of major effect in these areas as well. In ruffs (*Philomachus pugnax*), differences in social behavior and plumage color among three male morphs are explained by genetic differences in a single autosomal region where differences have accumulated in part owing to suppressed recombination within inversions (Lamichhaney et al. 2016). Likewise, in white-throated sparrows (*Zonotrichia albicollis*), differences in mating and parental care behaviors, as well as plumage differences between two morphs, are attributable to different alleles at a single large inversion-based supergene more than 100 million base pairs long (Tuttle et al. 2016). Although these two examples characterize stable polymorphisms within populations, they also demonstrate the strong potential for simple genetic bases for mating and parental care behavioral differences between species.

4.3. Sex Chromosomes

Although the examples discussed in Section 4.2 are mostly related to autosomes, evidence suggests that the Z chromosome, a sex chromosome that occurs singly in female birds and doubly in males, might play a disproportionate role (in comparison to its size in the genome) in behavioral isolation (Albert & Otto 2005, Ellegren 2009). Its sex-linked inheritance causes the Z chromosome to have a higher rate of substitution owing to a higher male mutation rate, less effective purging of deleterious mutations compared with autosomes, and more effective selection favoring some types of beneficial mutations (Charlesworth et al. 1987, Mank et al. 2009, Wright et al. 2015). This higher evolutionary rate means faster differentiation between populations and potentially more involvement in speciation [reviewed by Irwin (2018)].

In addition to this faster rate of evolution, the Z chromosome is expected to accumulate sexually antagonistic polymorphisms (Albert & Otto 2005, Charlesworth et al. 1987), in which one allele benefits females and another benefits males. Many of these polymorphisms could be related to behavioral traits, such as song or other displays. Two alleles involved in such a polymorphism reach stable equilibrium frequencies, based on the relative advantages of the two alleles in the two sexes. In this situation, a new allele at a second locus that confers a preference for one of the traits can spread through the population (Albert & Otto 2005). If the preference is Z-linked, a preference for a male-benefitting trait spreads, driving a similar shift in the trait itself. If the preference is autosomal, a preference for a female-benefitting trait spreads. It is not difficult to imagine how such dynamics occurring in different populations of a species could lead to differentiation and reproductive isolation between populations (Irwin 2018).

Empirical evidence for a large role of the Z chromosome in behavioral differentiation and speciation is growing. Approximately 22% of traits, some behavioral, that distinguish breeds of domesticated birds appear to be Z-linked, whereas the Z chromosome contains only approximately 2.7% of the whole genome (Edwards et al. 2005, Price 2002). In Gouldian finches, mating discrimination between two color morphs and plumage color traits (see **Table 1**) is Z-linked (Pryke 2010). Finally, female mating discrimination between male collared and pied flycatchers is Z-linked, as are the male traits that differ between the species (Sæther et al. 2007).

5. CONCLUSIONS AND FUTURE DIRECTIONS

5.1. Multimodal Signal Divergence and Speciation

Sexual selection for multiple ornaments can enhance reproductive isolation if multiple signals diverge and facilitate species recognition (Mead & Arnold 2004). As such, multimodal signal divergence could further enhance species recognition through simultaneous or sequential assessment of divergent signals. For example, the use of multimodal signals may provide more information and facilitate decision making more than the use of unimodal signals (Kulahci et al. 2008). In addition, multimodal signals may facilitate the sequential assessment of signals across different temporal and spatial scales, as the properties of different signaling modalities make each ideal for assessment or detection at different distances (Uy & Safran 2013). In the *Monarcha castaneiventris* flycatcher example discussed in Section 4, closely related taxa vary in both plumage color and song throughout the Solomon Islands. Field experiments indicated that song mediates the decision to approach, whereas plumage color mediates the decision to attack taxidermy mounts, suggesting that species recognition from a distance makes use of an acoustic signal, whereas species recognition at close range makes use of a visual signal (Uy & Safran 2013). Multimodal signals, therefore, provide the opportunity for sequential behavioral barriers (see also Greig et al. 2015). To date, limited empirical data address multimodal signal divergence and speciation in birds, despite the observation that many closely related taxa use both acoustic and visual signals in species recognition and mate choice (**Table 1**). Additional work is needed to determine how divergence in multimodal signals facilitates or even accelerates diversification and the evolution of enhanced behavioral isolation.

5.2. Genomic Architecture of Behavior and Speciation

As discussed in Section 4, unprecedented advances in sequencing and bioinformatics tools are providing unique insights into the genetic basis of morphological and behavioral traits involved in behavioral isolation. Candidate genes or genomic regions are identified by finding associations between traits and genetic variation. To go beyond correlation, the next necessary step is to validate these candidate genomic regions through functional experiments by directly establishing the effects of candidate mutations on trait expression (Hubbard et al. 2010).

A critical missing component in understanding the genetic basis of behavioral isolation is the genetic basis of mating preferences, which remains largely unknown. Although imprinting and learning are the major avenues of transmitting mating preferences in songbirds, recent genetic studies have revealed biases with respect to which signals to imprint (Wheatcroft & Qvarnström 2017). Uncovering the genetic basis of mating preferences should become more feasible as sequencing technologies and approaches from developmental biology become more readily available.

5.3. When Does Behavioral Isolation Lead to Distinct Species?

Even though reproductive isolation between pairs of descendent taxa increases with time since divergence (Coyne & Orr 1997), the efficacy of behavioral barriers in birds seems to depend more on the extent of phenotypic differences between signals rather than time since isolation. That is, several studies suggest that discrimination between homotypic and heterotypic signals is better predicted by differences in signal characteristics than time since divergence (Freeman & Montgomery 2017, Grant & Grant 1997, Sosa-Lopez et al. 2016, Tobias & Seddon 2009). Accordingly, given the importance of premating isolation to incipient speciation in birds, the likelihood that speciation between two taxa will reach completion might depend critically on the extent of signal divergence when (and if) allopatric populations come into secondary contact.

Finally, intrinsic postzygotic barriers are irreversible, whereas pre- and postzygotic behavioral isolation can be reversed. For example, in Darwin's finches of the genus *Camarhynchus* (tree finches), specimens collected on Floreana Island from 1852 to 1906 consisted of three genetically and morphologically distinct species. Resampling in 2005 and 2010 on the same island revealed that extensive hybridization had caused the collapse of the third species, resulting in only two genetically and morphologically distinct species and a third group of hybrids of the two (Kleindorfer et al. 2014). This example of a loss of a species through hybridization illustrates that even strong behavioral barriers are reversible, and as such, intrinsic postzygotic barriers may be necessary to complete the speciation process. In this context, pre- and postzygotic behavioral isolation can be critical to initiating speciation, thereby allowing for the eventual evolution of genetic incompatibilities to reach the final stages of speciation.

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LITERATURE CITED

Albert AY, Otto SP. 2005. Sexual selection can resolve sex-linked sexual antagonism. *Science* 310:119–21

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

Baack E, Melo MC, Rieseberg LH, Ortiz-Barrientos D. 2015. The origins of reproductive isolation in plants. *New Phytol*. 207:968–84

Badyaev AV, Young RL, Oh KP, Addison C. 2008. Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution* 62:1951–64

Baker MC. 1983. The behavioral response of female Nuttall's white-crowned sparrows to male song of natal and alien dialects. *Behav. Ecol. Sociobiol.* 12:309–15

Baker MC. 1991. Response to male indigo and lazuli buntings and their hybrids to song playback in allopatric and sympatric populations. *Behaviour* 119:225–42

Baker MC, Baker AEM. 1990. Reproductive behavior of female buntings: isolating mechanisms in a hybridizing pair of species. *Evolution* 44:332–38

Baker MC, Bjerke TK, Lampe HU, Espmark YO. 1987a. Sexual response of female yellowhammers to differences in regional song dialects and repertoire sizes. *Anim. Behav.* 35:395–401

Baker MC, Spitler-Nabors KJ, Thompson AD, Cunningham MA. 1987b. Reproductive behaviour of female white-crowned sparrows: effect of dialects and synthetic hybrid songs. *Anim. Behav.* 35:1766–74

Balaban E. 1988. Bird song syntax: learned intraspecific variation is meaningful. *PNAS* 85:3657–60

Baldassarre DT, Webster MS. 2013. Experimental evidence that extra-pair mating drives asymmetrical introgression of a sexual trait. *Proc. R. Soc. B* 280:20132175

Ballentine B, Horton B, Brown ET, Greenberg R. 2013. Divergent selection on bill morphology contributes to nonrandom mating between swamp sparrow subspecies. *Anim. Behav.* 86:467–73

Ballentine B, Searcy WA, Nowicki S. 2008. Reliable aggressive signalling in swamp sparrows. *Anim. Behav.* 75:693–703

Baptista LF, Schuchmann KL. 1990. Song learning in the Anna hummingbird (*Calypte anna*). *Ethology* 84:15–26

Barraclough TG, Harvey PH, Nee S. 1995. Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. B* 259:211–15

Barrera-Guzmán AO, Aleixo A, Shawkey MD, Weir JT. 2017. Hybrid speciation leads to novel male secondary sexual ornamentation of an Amazonian bird. *PNAS* 115:E218–25

Barton NH, Hewitt GM. 1985. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* 16:113–48

Bearhop S, Fiedler W, Furness RW, Votier SC, Waldron S, et al. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* 310:502–4

Benkman CW. 2003. Divergent selection drives the adaptive radiation of crossbills. *Evolution* 57:1176–81

Bensch S, Akesson S, Irwin DE. 2002. The use of AFLP to find an informative SNP: genetic differences across a migratory divide in willow warblers. *Mol. Ecol.* 11:2359–66

Bernal XE, Rand AS, Ryan MJ. 2007. Sex differences in response to nonconspecific advertisement calls: receiver permissiveness in male and female túngara frogs. *Anim. Behav.* 73:955–64

Berthold P, Querner U. 1981. Genetic basis of migratory behavior in European warblers. *Science* 212:77–79

Brainard MS, Doupe AJ. 2013. Translating birdsong: songbirds as a model for basic and applied medical research. *Annu. Rev. Neurosci.* 36:489–517

Brelsford A, Irwin DE. 2009. Incipient speciation despite little assortative mating: the yellow-rumped warbler hybrid zone. *Evolution* 63:3050–60

Catchpole CK, Slater PJ. 2003. *Bird Song: Biological Themes and Variations*. Cambridge, MA: Cambridge Univ. Press

Charlesworth B, Coyne J, Barton N. 1987. The relative rates of evolution of sex chromosomes and autosomes. *Am. Nat.* 130:113–46

Claramunt S, Derryberry EP, Remsen J, Brumfield RT. 2012. High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proc. R. Soc. B* 279:1567–74

Clayton N. 1990. Assortative mating in zebra finch subspecies, *Taeniopygia guttata* and *T. g. castanotis*. *Philos. Trans. R. Soc. B* 330:351–70

Cooke F, Finney G, Rockwell R. 1976. Assortative mating in lesser snow geese (*Anser caerulescens*). *Behav. Genet.* 6:127–40

Cooke F, McNally C. 1975. Mate selection and colour preferences in lesser snow geese. *Behaviour* 53:151–69

Cooper EA, Uy JAC. 2017. Genomic evidence for convergent evolution of a key trait underlying divergence in island birds. *Mol. Ecol.* 26:3760–74

Coyne JA, Orr HA. 1997. "Patterns of speciation in *Drosophila*" revisited. *Evolution* 51:295–303

Coyne JA, Orr HA. 2004. *Speciation*. Sunderland, MA: Sinauer

Cramer ER, Ålund M, McFarlane SE, Johnsen A, Qvarnström A. 2016. Females discriminate against heterospecific sperm in a natural hybrid zone. *Evolution* 70:1844–55

Curry CM, Patten MA. 2016. Shadow of a doubt: premating and postmating isolating barriers in a temporally complex songbird (Passeriformes: Paridae) hybrid zone. *Behav. Ecol. Sociobiol.* 70:1171–86

Danner JE, Danner RM, Bonier F, Martin PR, Small TW, Moore IT. 2011. Female, but not male, tropical sparrows respond more strongly to the local song dialect: implications for population divergence. *Am. Nat.* 178:53–63

Darwin C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: John Murray

Delmore KE, Irwin DE. 2014. Hybrid songbirds employ intermediate routes in a migratory divide. *Ecol. Lett.* 17:1211–18

Delmore KE, Kenyon HL, Germain RR, Irwin DE. 2015. Phenotypic divergence during speciation is inversely associated with differences in seasonal migration. *Proc. R. Soc. B* 282:20151921

Delmore KE, Liedvogel M. 2016. Investigating factors that generate and maintain variation in migratory orientation: a primer for recent and future work. *Front. Behav. Neurosci.* 10:3

Delmore KE, Toews DPL, Germain RR, Owens GL, Irwin DE. 2016. The genetics of seasonal migration and plumage color. *Curr. Biol.* 26:2167–73

Dobzhansky T. 1937. *Genetics and the Origin of Species*. New York: Columbia Univ. Press

Edwards SV, Kingan SB, Calkins JD, Balakrishnan CN, Jennings WB, et al. 2005. Speciation in birds: genes, geography, and sexual selection. *PNAS* 102:6550–57

Elgvin TO, Trier CN, Tørresen OK, Hagen IJ, Lien S, et al. 2017. The genomic mosaicism of hybrid speciation. *Sci. Adv.* 3:e1602996

Ellegren H. 2009. A selection model of molecular evolution incorporating the effective population size. *Evolution* 63:301–5

Feldman MW, Laland KN. 1996. Gene-culture coevolutionary theory. *Trends Ecol. Evol.* 11:453–57

Freeman BG, Montgomery GA. 2017. Using song playback experiments to measure species recognition between geographically isolated populations: a comparison with acoustic trait analyses. *Auk* 134:857–70

Gee JM. 2003. How a hybrid zone is maintained: behavioral mechanisms of interbreeding between California and Gambel's quail (*Callipepla californica* and *C. gambelii*). *Evolution* 57:2407–15

Grant BR, Grant PR. 1996. Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution* 50:2471–87

Grant PR, Grant BR. 1992. Hybridization of bird species. *Science* 256:193–97

Grant PR, Grant BR. 1997. Mating patterns of Darwin's finch hybrids determined by song and morphology. *Biol. J. Linn. Soc.* 60:317–43

Grant PR, Grant BR. 2007. *How and Why Species Multiply: The Radiation of Darwin's Finches*. Princeton, NJ: Princeton Univ. Press

Greig EI, Baldassarre DT, Webster MS. 2015. Differential rates of phenotypic introgression are associated with male behavioral responses to multiple signals. *Evolution* 69:2602–12

Greig EI, Webster MS. 2013. Spatial decoupling of song and plumage generates novel phenotypes between two avian subspecies. *Behav. Ecol.* 24:1004–13

Groth JG. 1993. *Evolutionary Differentiation in Morphology, Vocalizations, and Allozymes Among Nomadic Sibling Species in the North American Red Crossbill (Loxia curvirostra) Complex*. Berkeley: Univ. Calif. Press

Hauber ME, Russo SA, Sherman PW. 2001. A password for species recognition in a brood-parasitic bird. *Proc. R. Soc. B* 268:1041–48

Helbig A. 1996. Genetic basis, mode of inheritance and evolutionary changes of migratory directions in palaearctic warblers (Aves: Sylviidae). *J. Exp. Biol.* 199:49–55

Hill GE. 1994. Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. *Behav. Ecol.* 5:64–73

Hinde RA. 1959. Behaviour and speciation in birds and lower vertebrates. *Biol. Rev.* 34:85–127

Huang H, Rabosky DL. 2014. Sexual selection and diversification: reexamining the correlation between dichromatism and speciation rate in birds. *Am. Nat.* 184:E101–14

Hubbard JK, Uy JAC, Hauber ME, Hoekstra HE, Safran RJ. 2010. Vertebrate pigmentation: from underlying genes to adaptive function. *Trends Genet.* 26:231–40

Irwin DE. 2018. Sex chromosomes and speciation in birds and other ZW systems. *Mol. Ecol.* In press. **https://doi.org/10.1111/mec.14537**

Irwin DE, Irwin JH. 2005. Siberian migratory divides. In *Birds of Two Worlds: The Ecology and Evolution of Migration*, ed. R Greenberg, P Marra, pp. 27–40. Baltimore, MD: Johns Hopkins Univ. Press

Irwin DE, Price T. 1999. Sexual imprinting, learning and speciation. *Heredity* 82:347–54

Kaneshiro KY. 1980. Sexual isolation, speciation and direction of evolution. *Evolution* 34:437–44

Kennedy JD, Borregaard MK, Jønsson KA, Marki PZ, Fjeldså J, Rahbek C. 2016. The influence of wing morphology upon the dispersal, geographical distributions and diversification of the Corvides (Aves: Passeriformes). *Proc. R. Soc. B* 283:20161922

Kenyon HL, Alcaide M, Toews DPL, Irwin DE. 2017. Cultural isolation is greater than genetic isolation across an avian hybrid zone. *J. Evol. Biol.* 30:81–95

King AP, West MJ. 1977. Species identification in the North American cowbird: appropriate responses to abnormal song. *Science* 195:1002–4

King AP, West MJ, Eastzer DH. 1980. Song structure and song development as potential contributors to reproductive isolation in cowbirds (*Molothrus ater*). *J. Comp. Physiol. Psychol.* 94:1028

Kirschel AN, Blumstein DT, Smith TB. 2009. Character displacement of song and morphology in African tinkerbirds. *PNAS* 106:8256–61

Kleindorfer S, O'Connor JA, Dudaniec RY, Myers SA, Robertson J, Sulloway FJ. 2014. Species collapse via hybridization in Darwin's tree finches. *Am. Nat.* 183:325–41

Kroodsma D, Hamilton D, Sánchez JE, Byers BE, Fandiño-Mariño H, et al. 2013. Behavioral evidence for song learning in the suboscine bellbirds (*Procnias* spp.; Cotingidae). *Wilson J. Ornithol.* 125:1–14

Kulahci IG, Dornhaus A, Papaj DR. 2008. Multimodal signals enhance decision making in foraging bumblebees. *Proc. R. Soc. B* 275:797–802

Lackey A, Boughman J. 2013. Divergent sexual selection via male competition: Ecology is key. *J. Evol. Biol.* 26:1611–24

Lamichhaney S, Fan G, Widemo F, Gunnarsson U, Thalmann DS, et al. 2016. Structural genomic changes underlie alternative reproductive strategies in the ruff (*Philomachus pugnax*). *Nat. Genet.* 48:84–88

Lamichhaney S, Han F, Webster MT, Andersson L, Grant BR, Grant PR. 2017. Rapid hybrid speciation in Darwin's finches. *Science* 359:224–28

Langin KM, Sillett TS, Funk WC, Morrison SA, Desrosiers MA, Ghalambor CK. 2015. Islands within an island: repeated adaptive divergence in a single population. *Evolution* 69:653–65

Langin KM, Sillett TS, Morrison SA, Ghalambor CK. 2017. Bill morphology and neutral genetic structure both predict variation in acoustic signals within a bird population. *Behav. Ecol.* 28:866–73

Liedvogel M, Larson KW, Lundberg M, Gursoy A, Wassenaar LI, et al. 2014. No evidence for assortative mating within a willow warbler migratory divide. *Front. Zool.* 11:52

Lipshutz SE, Overcast IA, Hickerson MJ, Brumfield RT, Derryberry EP. 2017. Behavioural response to song and genetic divergence in two subspecies of white-crowned sparrows (*Zonotrichia leucophrys*). *Mol. Ecol.* 26:3011–27

López-Rull I, Lifshitz N, Garcia CM, Graves JA, Torres R. 2016. Females of a polymorphic seabird dislike foreign-looking males. *Anim. Behav.* 113:31–38

Lundberg M, Liedvogel M, Larson K, Sigeman H, Grahn M, et al. 2017. Genetic differences between willow warbler migratory phenotypes are few and cluster in large haplotype blocks. *Evol. Lett.* 1:155–68

Lyon BE, Eadie JM. 1991. Mode of development and interspecific avian brood parasitism. *Behav. Ecol.* 2:309–18

Mank JE, Nam K, Ellegren H. 2009. Faster-Z evolution is predominantly due to genetic drift. *Mol. Biol. Evol.* 27:661–70

Marshall JL, Arnold ML, Howard DJ. 2002. Reinforcement: the road not taken. *Trends Ecol. Evol.* 17:558–63

Mason NA, Burns KJ, Tobias JA, Claramunt S, Seddon N, Derryberry EP. 2017. Song evolution, speciation, and vocal learning in passerine birds. *Evolution* 71:786–96

Mayr E. 1942. *Systematics and the Origin of Species*. New York: Columbia Univ. Press

McEntee JP, Peñalba JV, Werema C, Mulungu E, Mbilinyi M, et al. 2016. Social selection parapatry in Afrotropical sunbirds. *Evolution* 70:1307–21

Mead LS, Arnold SJ. 2004. Quantitative genetic models of sexual selection. *Trends Ecol. Evol.* 19:264–71

Mortega KG, Flinks H, Helm B. 2014. Behavioural response of a migratory songbird to geographic variation in song and morphology. *Front. Zool.* 11:85

Mundinger PC. 1982. Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In *Acoustic Communication in Birds*, Vol. I, ed. DE Kroodsma, EH Miller, H Quellet, pp. 147–208. New York: Academic

Mundinger PC, Lahti DC. 2014. Quantitative integration of genetic factors in the learning and production of canary song. *Proc. R. Soc. B* 281:20132631

Nelson DA, Soha JA. 2004. Male and female white-crowned sparrows respond differently to geographic variation in song. *Behaviour* 141:53–69

Nicolakakis N, Sol D, Lefebvre L. 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. *Anim. Behav.* 65:445–52

Nottebohm F. 1972. The origins of vocal learning. *Am. Nat.* 106:116–40

Ottenburghs J, Kraus RH, Hooft P, Wieren SE, Ydenberg RC, Prins HH. 2017. Avian introgression in the genomic era. *Avian Res.* 8:30

Patten MA, Rotenberry JT, Zuk M. 2004. Habitat selection, acoustic adaptation, and the evolution of reproductive isolation. *Evolution* 58:2144–55

Payne RB, Payne LL, Woods JL. 1998. Song learning in brood-parasitic indigobirds *Vidua chalybeata*: song mimicry of the host species. *Anim. Behav.* 55:1537–53

Payne RB, Payne LL, Woods JL, Sorenson MD. 2000. Imprinting and the origin of parasite–host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. *Anim. Behav.* 59:69–81

Pearson SF, Rohwer S. 2000. Asymmetries in male aggression across an avian hybrid zone. *Behav. Ecol.* 11:93–101

Phillimore AB, Freckleton RP, Orme CDL, Owens IP. 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. *Am. Nat.* 168:220–29

Podos J. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* 409:185–88

Poelstra JW, Vijay N, Bossu CM, Lantz H, Ryll B, et al. 2014. The genomic landscape underlying phenotypic integrity in the face of gene flow in crows. *Science* 344:1410–14

Presgraves DC. 2002. Patterns of postzygotic isolation in Lepidoptera. *Evolution* 56:1168–83

Price T. 2007. *Speciation in Birds*. Greenwood Village, CO: Roberts & Co.

Price TD. 2002. Domesticated birds as a model for the genetics of speciation by sexual selection. *Genetica* 116:311–27

Price TD, Bouvier MM. 2002. The evolution of F-1 postzygotic incompatibilities in birds. *Evolution* 56:2083–89

Pryke SR. 2010. Sex chromosome linkage of mate preference and color signal maintains assortative mating between interbreeding finch morphs. *Evolution* 64:1301–10

Pryke SR, Griffith SC. 2007. The relative role of male vs. female mate choice in maintaining assortative pairing among discrete colour morphs. *J. Evol. Biol.* 20:1512–21

Pryke SR, Griffith SC. 2009. Postzygotic genetic incompatibility between sympatric color morphs. *Evolution* 63:793–98

Qvarnström A, Haavie J, Saether S, Eriksson D, Pärt T. 2006. Song similarity predicts hybridization in flycatchers. *J. Evol. Biol.* 19:1202–9

Ratcliffe LM, Grant PR. 1983. Species recognition in Darwin's finches (*Geospiza*, Gould). II. Geographic variation in mate preference. *Anim. Behav.* 31:1154–65

Ravinet M, Faria R, Butlin R, Galindo J, Bierne N, et al. 2017. Interpreting the genomic landscape of speciation: a road map for finding barriers to gene flow. *J. Evol. Biol.* 30:1450–77

Ritchie MG. 2007. Sexual selection and speciation. *Annu. Rev. Ecol. Evol. Syst.* 38:79–102

Rohwer S, Irwin DE. 2011. Molt, orientation, and avian speciation. *Auk* 128:419–25

Rolshausen G, Segelbacher G, Hobson KA, Schaefer HM. 2009. Contemporary evolution of reproductive isolation and phenotypic divergence in sympatry along a migratory divide. *Curr. Biol.* 19:2097–101

Rowley I, Chapman G. 1986. Cross-fostering, imprinting and learning in two sympatric species of cockatoo. *Behaviour* 96:1–16

Ruegg KC, Smith TB. 2002. Not as the crow flies: a historical explanation for circuitous migration in Swainson's thrush (*Catharus ustulatus*). *Proc. R. Soc. B* 269:1375–81

Sæther SA, Sætre G-P, Borge T, Wiley C, Svedin N, et al. 2007. Sex chromosome-linked species recognition and evolution of reproductive isolation in flycatchers. *Science* 318:95–97

Sætre G-P, Saether SA. 2010. Ecology and genetics of speciation in *Ficedula* flycatchers. *Mol. Ecol.* 19:1091–106

Sætre G-P, Moum T, Bures S, Kral M, Adamjan M, Moreno J. 1997. A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* 387:589–92

Safran RJ, Vortman Y, Jenkins BR, Hubbard JK, Wilkins MR, et al. 2016. The maintenance of phenotypic divergence through sexual selection: an experimental study in barn swallows *Hirundo rustica*. *Evolution* 70:2074–84

Searcy WA. 1990. Species recognition of song by female red-winged blackbirds. *Anim. Behav.* 40:1119–27

Searcy WA, Nowicki S, Hughes M. 1997. The response of male and female song sparrows to geographic variation in song. *Condor* 99:651–57

Secondi J, Bretagnolle V, Compagnon C, Faivre B. 2003. Species-specific song convergence in a moving hybrid zone between two passerines. *Biol. J. Linn. Soc.* 80:507–17

Seddon N, Tobias JA. 2010. Character displacement from the receiver's perspective: species and mate recognition despite convergent signals in suboscine birds. *Proc. R. Soc. B* 277:2475–83

Servedio MR, Boughman JW. 2017. The role of sexual selection in local adaptation and speciation. *Annu. Rev. Ecol. Evol. Syst.* 48:85–109

Servedio MR, Van Doorn GS, Kopp M, Frame AM, Nosil P. 2011. Magic traits in speciation: 'magic' but not rare? *Trends Ecol. Evol.* 26:389–97

Short LL. 1969. Taxonomic aspects of avian hybridization. *Auk* 86:84–105

Slagsvold T, Hansen BT, Johannessen LE, Lifjeld JT. 2002. Mate choice and imprinting in birds studied by cross-fostering in the wild. *Proc. R. Soc. B* 269:1449–55

Slagsvold T, Wiebe KL. 2011. Social learning in birds and its role in shaping a foraging niche. *Philos. Trans. R. Soc. B* 366:969–77

Smith BT, McCormack JE, Cuervo AM, Hickerson MJ, Aleixo A, et al. 2014. The drivers of tropical speciation. *Nature* 515:406–9

Smith DG. 1972. The role of the epaulets in the red-winged blackbird (*Agelaius phoeniceus*) social system. *Behaviour* 41:251–68

Smith JW, Benkman CW. 2007. A coevolutionary arms race causes ecological speciation in crossbills. *Am. Nat.* 169:455–65

Smith JW, Sjoberg SM, Mueller MC, Benkman CW. 2012. Assortative flocking in crossbills and implications for ecological speciation. *Proc. R. Soc. B* 279:4223–29

Snowberg L, Benkman C. 2007. The role of marker traits in the assortative mating within red crossbills, *Loxia curvirostra* complex. *J. Evol. Biol.* 20:1924–32

Sorenson MD, Hauber ME, Derrickson SR. 2010. Sexual imprinting misguides species recognition in a facultative interspecific brood parasite. *Proc. R. Soc. B* 277:3079–85

Sorenson MD, Sefc KM, Payne RB. 2003. Speciation by host switch in brood parasitic indigobirds. *Nature* 424:928–31

Sosa-Lopez JR, Martinez Gomez JE, Mennill DJ. 2016. Divergence in mating signals correlates with genetic distance and behavioural responses to playback. *J. Evol. Biol.* 29:306–18

Svedin N, Wiley C, Veen T, Gustafsson L, Qvarnström A. 2008. Natural and sexual selection against hybrid flycatchers. *Proc. R. Soc. B* 275:735–44

Tietze DT, Wassmann C, Martens J. 2012. Territorial song does not isolate Yellowhammers (*Emberiza citrinella*) from Pine Buntings (*E. leucocephalos*). *Vertebr. Zool.* 62:113–22

Tobias JA, Seddon N. 2009. Signal design and perception in *Hypocnemis* antbirds: evidence for convergent evolution via social selection. *Evolution* 63:3168–89

Toews DPL, Campagna L, Taylor SA, Balakrishnan CN, Baldassarre DT, et al. 2016a. Genomic approaches to understanding population divergence and speciation in birds. *Auk* 133:13–30

Toews DPL, Taylor SA, Vallender R, Brelsford A, Butcher BG, et al. 2016b. Plumage genes and little else distinguish the genomes of hybridizing warblers. *Curr. Biol.* 26:2313–18

Turbek SP, Scordato ES, Safran RJ. 2017. The role of seasonal migration in population divergence and reproductive isolation. *Trends Ecol. Evol.* 33:164–75

Tuttle EM, Bergland AO, Korody ML, Brewer MS, Newhouse DJ, et al. 2016. Divergence and functional degradation of a sex chromosome-like supergene. *Curr. Biol.* 26:344–50

Uy JAC, Cooper EA, Cutie S, Concannon MR, Poelstra JW, et al. 2016. Mutations in different pigmentation genes are associated with parallel melanism in island flycatchers. *Proc. R. Soc. B* 283:20160731

Uy JAC, Safran RJ. 2013. Variation in the temporal and spatial use of signals and its implications for multimodal communication. *Behav. Ecol. Sociobiol.* 67:1499–511

Veen T, Borge T, Griffith SC, Saetre G-P, Bures S, et al. 2001. Hybridization and adaptive mate choice in flycatchers. *Nature* 411:45

Verzijden MN, Ten Cate C, Servedio MR, Kozak GM, Boughman JW, Svensson EI. 2012. The impact of learning on sexual selection and speciation. *Trends Ecol. Evol.* 27:511–19

von Rönn JA, Shafer A, Wolf JB. 2016. Disruptive selection without genome-wide evolution across a migratory divide. *Mol. Ecol.* 25:2529–41

Vortman Y, Lotem A, Dor R, Lovette I, Safran RJ. 2013. Multiple sexual signals and behavioral reproductive isolation in a diverging population. *Am. Nat.* 182:514–23

Warren W, Clayton D, Ellegren H, Arnold A, Hillier L, et al. 2010. The genome of a songbird. *Nature* 464:757–62

Warriner CC, Lemmon WB, Ray TS. 1963. Early experience as a variable in mate selection. *Anim. Behav.* 11:221–24

West-Eberhard MJ. 1983. Sexual selection, social competition and speciation. *Q. Rev. Biol.* 58:155–83

Wheatcroft D, Qvarnström A. 2017. Genetic divergence of early song discrimination between two young songbird species. *Nat. Ecol. Evol.* 1:0192

Whitney O, Pfenning AR, Howard JT, Blatti CA, Liu F, et al. 2014. Core and region-enriched networks of behaviorally regulated genes and the singing genome. *Science* 346:1256780

Willett CS. 2011. The nature of interactions that contribute to postzygotic reproductive isolation in hybrid copepods. *Genetica* 139:575–88

Wilson A, Maxson LR, Sarich V. 1974. Two types of molecular evolution. Evidence from studies of interspecific hybridization. *PNAS* 71:2843–47

Wright AE, Harrison PW, Zimmer F, Montgomery SH, Pointer MA, Mank JE. 2015. Variation in promiscuity and sexual selection drives avian rate of Faster-Z evolution. *Mol. Ecol.* 24:1218–35

Wu CI. 2001. The genic view of the process of speciation. *J. Evol. Biol.* 14:851–65

Yasukawa K, Butler LK, Enstrom DA. 2009. Intersexual and intrasexual consequences of epaulet colour in male red-winged blackbirds: an experimental approach. *Anim. Behav.* 77:531–40

Annual Review of
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Contents

Behavioral Isolation and Incipient Speciation in Birds
J. Albert C. Uy, Darren E. Irwin, and Michael S. Webster 1

The Ecology and Evolution of Alien Plants
Mark van Kleunen, Oliver Bossdorf, and Wayne Dawson 25

Biodiversity and Functional Ecology of Mesophotic Coral Reefs
Michael P. Lesser, Marc Slattery, and Curtis D. Mobley 49

Evolutionary Conflict
David C. Queller and Joan E. Strassmann 73

Evaluating Model Performance in Evolutionary Biology
Jeremy M. Brown and Robert C. Thomson 95

Plant Secondary Metabolite Diversity and Species Interactions
André Kessler and Aino Kalske 115

Variation and Evolution of Function-Valued Traits
Richard Gomulkiewicz, Joel G. Kingsolver, Patrick A. Carter, and Nancy Heckman 139

Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates
Susanne S. Renner and Constantin M. Zohner 165

Bivalve Impacts in Freshwater and Marine Ecosystems
Caryn C. Vaughn and Timothy J. Hoellein 183

Uses and Misuses of Environmental DNA in Biodiversity Science and Conservation
Melania E. Cristescu and Paul D.N. Hebert 209

Frontiers in Metapopulation Biology: The Legacy of Ilkka Hanski
Otso Ovaskainen and Marjo Saastamoinen 231

Integrating Networks, Phylogenomics, and Population Genomics for the Study of Polyploidy
Paul D. Blischak, Makenzie E. Mabry, Gavin C. Conant, and J. Chris Pires 253

Ecological Response to Permafrost Thaw and Consequences for Local and Global Ecosystem Services
Edward A.G. Schuur and Michelle C. Mack 279

(Non)Parallel Evolution
Daniel I. Bolnick, Rowan D.H. Barrett, Krista B. Oke, Diana J. Rennison, and Yoel E. Stuart 303

Mechanisms of Plastic Rescue in Novel Environments
Emilie C. Snell-Rood, Megan E. Kobiela, Kristin L. Sikkink, and Alexander M. Shephard 331

Challenging Dogma Concerning Biogeographic Patterns of Antarctica and the Southern Ocean
Kenneth M. Halanych and Andrew R. Mahon 355

Dinosaur Macroevolution and Macroecology
Roger B.J. Benson 379

Life in Dry Soils: Effects of Drought on Soil Microbial Communities and Processes
Joshua P. Schimel 409

Using Genomic Data to Infer Historic Population Dynamics of Nonmodel Organisms
Annabel C. Beichman, Emilia Huerta-Sanchez, and Kirk E. Lohmueller 433

The Contemporary Evolution of Fitness
Andrew P. Hendry, Daniel J. Schoen, Matthew E. Wolak, and Jane M. Reid 457

The Deep Past Controls the Phylogenetic Structure of Present, Local Communities
Pille Gerhold, Marcos B. Carlucci, Şerban Procheş, and Andreas Prinzing 477

Development and Evolutionary Constraints in Animals
Frietson Galis, Johan A.J. Metz, and Jacques J.M. van Alphen 499

Indexes

Cumulative Index of Contributing Authors, Volumes 45–49 523

Cumulative Index of Article Titles, Volumes 45–49 527

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at http://www.annualreviews.org/errata/ecolsys