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Incorporating the full annual cycle when studying reproductive isolation and speciation

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As individual tracking devices and year-round genetic sampling become more accessible, research on the historically understudied nonbreeding period has exploded in the past decade. These studies are revealing tremendous inter- and intraspecific variation in migratory, molting, and other nonbreeding strategies, thereby informing efforts to protect bird populations throughout the entire annual cycle. However, we still have much to learn about where and when nonbreeding adaptive variation influences reproductive isolation and speciation. Previous work has demonstrated that some adaptations to conditions in different nonbreeding areas or migratory routes can fuel diversification by precluding opportunities for diverging lineages to interbreed or, in instances where lineages do interbreed, manifesting as disadvantageous phenotypes in hybrids. In this paper, we provide an overview of both established and speculative processes through which the primary nonbreeding events in the avian annual cycle (i.e. molt, migration, and overwintering) may interact to regulate gene flow between avian lineages. Although the relatively few but well-described examples of divergence in nonbreeding phenotypes contributing to reproductive isolation suggest nonbreeding divergence is a common mode of speciation in birds, a growing number of population genetic studies reporting nonbreeding divergence in the absence of reproductive isolation seemingly suggest the opposite conclusion. We outline processes that could result in this apparent contradiction and propose general comparative frameworks to test factors that may predictably mediate the relationship between nonbreeding divergence and reproductive isolation. In the past, a shortage of nonbreeding natural history and population genetic data have impeded our ability to test these predictions in more than just a few systems. We urge evolutionary biologists to pay closer attention to conservation-oriented studies, which are rapidly filling these knowledge gaps and presenting opportunities to better understand the true role of nonbreeding divergence in avian diversification.

Keywords: diversification, migration, molt, nonbreeding, reproductive isolation, speciation

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Introduction

Successful reproduction and survival from one year to the next requires finely-tuned integration of physiological, behavioral, and life-history traits. An individual must align resource demands with periods of sufficient resource availability while appropriately balancing investment between reproduction and self-maintenance to maximize lifetime fitness (Buehler and Piersma 2008). To help individuals meet these challenges in different fitness landscapes, avian populations have evolved diverse strategies for breeding, molting, migrating, and surviving between breeding periods (Rohwer and Irwin 2011). Disruptions during any of these events have the potential to compromise performance during the rest of the year, reducing reproductive output and increasing mortality risk (Senner et al. 2015). Given the potential for these disruptions to precipitate population declines, recent decades have seen an explosion of research aimed at identifying and mitigating anthropogenic disturbance at different stages of the annual cycle. These studies have linked population declines with destruction of nonbreeding habitat (Rappole et al. 2003, Marra et al. 2015b, Kramer et al. 2018), hazards on migration routes (Klaassen et al. 2014, Palacín et al. 2017, Newton 2025), and phenological mismatches between resource demand and availability during molt (Dougherty 2023).

While this full annual cycle perspective is now well entrenched in conservation research, it remains less common in studies of avian speciation and diversification. Perhaps because ornithologists rely primarily on the biological species concept to demarcate avian lineages from one another, most studies exploring speciation in birds have focused on the contribution of breeding phenotypes to reproductive isolation between populations (Mayr 1963, McKitrick and Zink 1988, Coyne and Orr 2004, Price 2008). However, because nonbreeding phenotypes determine which individuals survive between breeding periods and the condition of these individuals at the start of breeding, they inherently influence reproductive isolation. Some empirical studies and phylogenetic analyses have documented specific mechanisms by which nonbreeding adaptive divergence can restrict gene flow between avian lineages (Ruegg 2007, Gómez-Bahamón et al. 2020, Dougherty 2023). We group these mechanisms into two categories. First, adaptive divergence in molt, migration, and other strategies aimed at tracking different spatiotemporal patterns in resource availability during nonbreeding periods can carry over to influence breeding locations and phenology, in turn precluding opportunities for lineages to interbreed (Taylor and Friesen 2017). Second, when previously isolated populations come into secondary contact and are able to interbreed, adaptive differences in nonbreeding strategies may mediate effective gene flow by influencing sexual signals, manifesting as novel phenotypes in hybrids (in this manuscript, we use the term 'hybrid' to refer to a first-generation descendant of crosses between two different genetic lineages), and in turn determining selection on mating preferences (Delmore and Irwin 2014, Kopp et al. 2018). At the same time, some population genetic studies suggest that nonbreeding divergence may not always result in speciation (Jamieson and Ydenberg 2009, Kraus et al. 2012, Sanchez-Donoso et al. 2022, Christie et al. 2023). This apparent contradiction raises the following questions: 1) What types of nonbreeding divergence promote reproductive isolation? 2) What determines whether or not nonbreeding divergence contributes to reproductive isolation? 3) How can nonbreeding divergence exist without reproductive isolation? 4) How often does nonbreeding divergence actually promote speciation?

In this review, we address these questions by first outlining both established and speculative mechanisms by which adaptive variation with respect to the primary nonbreeding events in the avian annual cycle (i.e. molt, migration, and overwintering) can regulate gene flow between lineages. In doing so, we identify specific aspects of nonbreeding phenotypes on which more research is needed to understand their role in speciation. We focus primarily on temperate-breeding taxa, as comparatively few studies have documented nonbreeding adaptive variation in tropical taxa (but that is not to say that nonbreeding conditions do not influence diversification in the tropics) (Rohwer and Irwin 2011). Importantly, while previous reviews have outlined established mechanisms by which seasonal migration influences reproductive isolation and population divergence (Turbek et al. 2018), our review focuses specifically on the interactions between migration and other avian life history traits. After overviewing instances where nonbreeding adaptive divergence seemingly promotes reproductive isolation, we then discuss instances where it seemingly does not. In making this contrast, we identify potentially universal factors that determine whether nonbreeding divergence influences reproductive isolation. Finally, we overview ways for future studies to test these predictions with rapidly expanding datasets.

How can nonbreeding divergence restrict opportunities for lineages to interbreed and enhance prezygotic reproductive isolation?

Spatial and temporal isolation

The foremost determinant of reproductive isolation between lineages is whether they have the opportunity to interbreed (Coyne and Orr 2004). Different nonbreeding conditions may select for differences in migratory strategies, which may carry over to influence breeding location and phenology, thereby eliminating the potential for diverging lineages to interbreed altogether and promoting speciation. Phylogenetic analyses have demonstrated that gains and losses of seasonal migration occur frequently in at least some avian families as populations adapt in response to changes in nonbreeding resource availability (Winger et al. 2011, Rolland et al. 2014), perhaps enabled by diverse expression–regulation mechanisms governing migratory phenotype (Caballero-Lopez and Bensch 2024). Regardless of whether a population evolves to become sedentary or migratory, a novel strategy (as well as associated changes in physiology, behavior, and morphology) may result in a geographically distinct breeding location from populations with ancestral migratory phenotypes. Recent studies have reported abundant evidence of speciation via migratory drop-off, in which resident populations become isolated from migratory ancestors (Gómez-Bahamón et al. 2020, Dufour et al. 2024). Even when a shift in migratory strategy does not result in distinct breeding areas, it can still reduce opportunities for hybridization by influencing breeding phenology. Individuals that do not migrate or migrate short distances between breeding and nonbreeding areas usually initiate breeding earlier than individuals that migrate longer distances (Bearhop et al. 2005). In turn, individuals with similar breeding phenology are more likely to interbreed (Brewer et al. 2020). Given the high potential for allochronic isolation with variation in migratory distance, changing migratory behavior is likely a widespread mode of speciation in birds (Taylor and Friesen 2017).

Divergence in sexual signals

Birds often mate assortatively on the basis of sexual signals (e.g. plumage and song), such that sexual selection coupled with preference for matching phenotypes promotes reproductive isolation and speciation in sympatry (Tomback and Baker 1984, Baker and Baker 1990, Semenov et al. 2017, Kopp et al. 2018). Breeding plumage quality, a near-universal predictor of reproductive success (Gill 2007), may represent an honest signal of resource availability during molt (Keyser and Hill 1999, 2000, Reudink et al. 2009b). Therefore, sexual selection in birds may frequently operate in part by favoring strategies that enable individuals to access resources necessary for supplying the development of attractive breeding phenotypes prior to breeding (Trivers 1976, West-Eberhard 1983, Norris et al. 2004, Reudink et al. 2009a). Given the now well-established connection between nonbreeding conditions and breeding phenotypes, we hypothesize that there are many potential mechanisms by which adaptations to different nonbreeding conditions can influence sexual signals and enable prezygotic reproductive isolation. If individuals experience different resource availability or phenology during nonbreeding periods, populations may consequently evolve different breeding plumage characteristics. For example, populations with access to ample resources prior to breeding may evolve an extensive prealternate molt, potentially resulting in strikingly different breeding plumage than populations that replace fewer or no feather tracts before breeding. Furthermore, recent research has demonstrated that the extent of prealternate molt correlates with migratory distance, long-distance migrants that spend nonbreeding periods in areas with longer days have more time to forage and supply feather growth, and also suffer increased ultra-violet radiation exposure, which damages feathers and necessitates replacement (Terrill et al. 2020, Pageau et al. 2021). This heightened potential for interpopulation breeding plumage divergence is perhaps augmented by stronger sexual selection on males in taxa that migrate longer distances (Catchpole 1980, Badyaev and Hill 2003). In summary, while several studies have linked nonbreeding conditions with variation in breeding phenotypes, and other studies have linked variation in breeding phenotypes with assortative mating and prezygotic reproductive isolation, more research is needed to describe a potential causal pathway linking nonbreeding conditions, nonbreeding adaptations, breeding phenotypes, and reproductive isolation.

The pathway linking nonbreeding conditions and prezygotic reproductive isolation has been described more concretely with respect to song. For example, marsh warblers *Acrocephalus palustris* learn to mimic songs that they hear in their nonbreeding territories. Because females prefer songs from their own nonbreeding territories, assortative mating corresponds to migratory strategy (Dowsett-Lemaire 1979). Furthermore, lower resource availability during nonbreeding periods may select for specialized feeding morphology targeting reliable food sources (Liem 1980, Grant and Grant 1990). Periods of resource scarcity likely spurred the evolution of divergent bill structure within Darwin's finches *Geospiza* and red crossbills *Loxia curvirostra* (Schluter and Grant 1984, Benkman 1993). Variation in bill size and shape in turn influences vocalizations and song performance during breeding periods (Podos et al. 2004, Huber et al. 2006, Podos and Schroeder 2024).

How can nonbreeding divergence promote postzygotic reproductive isolation?

Selection to track resources and avoid hazards during nonbreeding periods favors the evolution of different co-adapted trait complexes in parental populations (Dingle 2006, Liedvogel and Lundberg 2014). When prezogotic barriers do not prevent hybridization between populations, these nonbreeding adaptive syndromes may break down in hybrids, resulting in novel phenotypic combinations (Dougherty 2023). Hybrids may thus suffer elevated mortality rates during nonbreeding periods or, by tracking resources less efficiently, suffer compounding delays at successive stages of the annual cycle that ultimately reduce breeding success. If hybrid phenotypes are disadvantageous, they will restrict introgression between parental populations and may select for the reinforcement of prezygotic reproductive barriers (Coyne and Orr 2004). Below, we overview how adaptive divergence at each stage of the annual cycle could reduce hybrid fitness.

Migration and molt

Many previous studies (and reviews) have established interpopulation divergence in migratory orientation as a potent mechanism of postzygotic reproductive isolation in birds (Helbig 1996, Winker 2010, Rohwer and Irwin 2011, Scordato et al. 2020). In short, orientation divides occur when two lineages breed sympatrically but navigate in opposite directions around a shared barrier during migration. When migratory routes are predominantly inherited rather than learned, as is understood to be the case for most passerines, the mixture of alleles in hybrids may result in intermediate orientation directly towards the barrier (Helbig 1991, 1996, Ruegg 2007). Extensive documentation of putatively disadvantageous hybrid phenotypes and population genetic structure near migratory barriers throughout the world – e.g. the Mediterranean Sea: Helbig et al. (1989); the Tibetan Plateau: Scordato et al. (2020); and the Great Basin Western North America: Delmore and Irwin (2014) – suggest orientation divergence is likely a widespread mechanism of postzygotic reproductive isolation in migratory birds.

Despite extensive exploration of hybrid phenotypes in orientation divides, few studies have attempted to describe how adaptive divergence in other aspects of the avian migratory program potentially influence postzygotic reproductive isolation. Earlier studies and reviews have speculated that adaptive divergence in molt phenology and location may have particularly important consequences for relative hybrid fitness (Rohwer and Manning 1990, Rohwer and Irwin 2011). The annual full-body molt, which typically occurs following the breeding period, represents one of the most metabolically demanding events in the avian annual cycle (Dolnik and Gavrilov 1979, Murphy and Taruscio 1995, Gill 2007). To meet the demands of feather protein synthesis, avian populations have evolved to molt at times and locations with sufficient resources. Migratory populations, which experience different patterns of resource availability throughout the year, have evolved tremendous variation in relative molt phenology. For example, most migratory passerines that breed in eastern North America molt prior to postbreeding migration, allowing them to migrate with fresh, strong feathers (Yuri and Rohwer 1997, Rohwer and Irwin 2011). In contrast, low primary productivity in late summer throughout western North America has selected for populations that breed in this half of the continent to molt during an extended migratory stopover in monsoonal regions (Rohwer and Manning 1990, Voelker and Rohwer 1998, Pageau et al. 2020). Our work on captive birds demonstrated that some hybrids between taxa with different molt and migration phenology exhibit novel strategies, potentially attempting to replace flight feathers during migration (Dougherty and Carling unpubl.). If these novel strategies force hybrids to molt at times or locations without sufficient resources, they may struggle to supply feather growth and suffer higher mortality rates (Murphy et al. 1988, Holmgren and Hedenström 1995, Saino et al. 2013). Supporting this prediction, comparisons of age ratios in museum specimens suggests lower survivorship in hybrids between populations with different relative molt and migration phenology than in hybrids between populations with similar molting strategies (Rohwer et al. 2023). Furthermore, even if hybrids do survive to the next breeding season, the association between resource availability during molt and breeding plumage quality implies that hybrids molting at inopportune times or locations may be less successful than unadmixed individuals in securing territories or mates (Norris et al. 2004).

Other nonbreeding phenotypes

Regardless of adaptive divergence between parental taxa, endogenous genomic incompatibilities can exacerbate selection against hybrids at all stages of the annual cycle. However, if endogenous characteristics of hybrids either increase their metabolic demands or cause them to track resources less efficiently, we speculate that the cost of these incompatibilies may be most severe during nonbreeding periods when resource availability may be lower. Although documented in only a few systems, mismatch between mitochondrial and nuclear gene products is likely a widespread source of selection against avian hybrids (McDiarmid et al. 2024). Combinations of nuclear and mitochondrial variants from two distinct parental populations may result in inefficient cellular respiration, scaling up to elevate the organism's basal metabolic rate (Olson et al. 2010, Taylor et al. 2014). Hybrids may struggle to meet these increased energetic costs on top of already demanding events, such as migration or molt, or during periods of resource scarcity, such as temperate winters. Disadvantageous hybrid migration or molting strategies may further compound this challenge. Nuclear Bateson–Dobzhansky–Muller incompatibilities, negative epistatic interactions between genetic variants from different parental populations that interfere with normal development and function (Schumer et al. 2015), may similarly increase hybrid mortality risk during nonbreeding periods. For instance, reduced hippocampal neurogenesis in hybrid chickadees impairs their cognitive performance and memory, likely challenging them to find sufficient resources during harsh winters (McQuillan et al. 2018). Future research is needed to test the prediction that endogenous incompatibilities elevate hybrid mortality primarily during nonbreeding periods.

Counterexamples: how can nonbreeding divergence exist without reproductive isolation?

Despite abundant evidence that nonbreeding adaptive divergence can maintain reproductive isolation and accelerate speciation between diverging lineages, population genetic studies have identified a number of systems in which nonbreeding divergence seemingly occurs in the absence of reproductive isolation. For instance, some shorebird species exhibit tremendous intraspecific variation in migratory routes and molting phenology yet surprisingly weak population genetic structure (Jamieson and Ydenberg 2009, Christie et al. 2023). Furthermore, migratory taxa often exhibit weaker population structure than resident taxa despite much greater variation in nonbreeding strategies (Arguedas and Parker 2000, Sanchez-Donoso et al. 2022).

A likely explanation for this contradiction is that, while seasonal migration can introduce variation in nonbreeding strategies between diverging lineages, certain attributes of migration may counteract the resulting reduction in breeding opportunities and hybrid fitness costs by increasing the likelihood that lineages will interbreed The brief breeding period available to long-distance migrants may synchronize breeding phenology among sympatric populations, regardless of nonbreeding divergence (Pedersen et al. 2020). As a result, migratory individuals may have increased opportunity for extra-pair copulations with heterospecifics (Spottiswoode and Møller 2004). Even when populations typically breed in different locations, shared environmental barriers and resources may result in convergence of migratory routes (Cohen and Satterfield 2020). In populations or age classes with low fidelity to breeding sites, information transfer among heterospecifics during prebreeding migration could precipitate breeding sympatry (Mukhin et al. 2008). Similarly, migration introduces the potential for gene flow via postnatal dispersal and vagrancy (Christie et al. 2023, Tonelli et al. 2023). When individuals occur outside their population's typical breeding distribution, the absence of conspecific mates frequently results in breeding with heterospecifics (Ottenburghs et al. 2016, Moore and Coulson 2020).

In addition to increasing opportunities for hybridization, migration may also weaken individual preferences for conspecifics. A short breeding period selects for heightened plasma testosterone levels in males (Moore et al. 2002, Garamszegi et al. 2005, 2008), spurring them to pursue mating opportunities more aggressively and perhaps less discriminately (Ketterson and Nolan 1992). Male preference for conspecific females may be further weakened by the fact that longer migratory distance selects for more cryptic, potentially conserved plumage in females (Simpson et al. 2015). Stronger sexual selection may also skew female preference in favor of more extreme breeding phenotypes, which may occur in heterospecifics (Price 2006). Furthermore, the risks incurred during migration may elevate adult mortality risk, resulting in a faster life history than tropical resident populations (Rushing et al. 2017, Jahn et al. 2020). If migratory individuals have fewer opportunities to breed over their shorter lifetimes, selection may favor less discriminating sexual preferences, when a bird has a low likelihood of surviving to the next breeding period, it may be more likely to mate with whatever potential partners are available, including heterospecifics, than forgo breeding in unfavorable years (Wilson and Hendrick 1982, Otto et al. 2008). The full extent to which these mechanisms facilitate gene flow and dampen diversification rates in migratory lineages requires future study.

Knowledge gaps and future directions

How much nonbreeding adaptive variation actually exists?

To understand the potential for adaptive divergence at any stage of the annual cycle to impose reproductive isolation between populations, we must first describe adaptive divergence. Given ornithology's historic focus on breeding populations, we still have much to learn about natural history variation during migration, molt, and the rest of the nonbreeding period for even common and frequently studied species (Leu and Thompson 2002, Marra et al. 2015a, Kiat 2023). While quantifying natural history variation throughout the annual cycle presents a daunting task, new technologies are rapidly enabling researchers to address these gaps in a variety of systems (Rakhimberdiev et al. 2016, Kramer et al. 2018, Savides 2022). Tracking devices, such as light-level geolocators (Kramer et al. 2018, Senner et al. 2019) and the Motus network (Taylor et al. 2017, Blain et al. 2024) for small passerines and satellite transmitters for larger species (Phillips et al. 2003, Pierce et al. 2021), can yield daily location data for individual birds throughout the year, allowing researchers to identify migratory routes, nonbreeding sites, and stopover locations putatively important for refueling or molt. However, these technologies have limitations. Daily location estimates from geolocators can have high uncertainty, especially around the equinox and near the equator (Delmore and Irwin 2014, Savides 2022), and Motus detections are dependent on the density of Motus towers, which is still sparse in most of the world (Blain et al. 2024). Stable isotope ratios generated from feather and claw samples can also shed light on general molting and nonbreeding locations (Toews et al. 2014). While most studies describing natural history at understudied stages of the annual cycle aim to strengthen conservation strategies, they incidentally generate questions and identify appropriate systems for evolutionary biologists interested in speciation, systems with high intra- or interspecific variation in molt, migration, or nonbreeding location combined with strong individual fidelity to nonbreeding areas (i.e. strong migratory connectivity) are good candidates for investigating how nonbreeding phenotypes influence reproductive isolation and population divergence (Cohen et al. 2018).

Exploring the extent to which this nonbreeding divergence contributes to reproductive isolation also requires knowledge of species boundaries and population genetic structure. Thankfully, conservation genetic studies are rapidly quantifying migratory connectivity and population structure throughout the annual cycle for a variety of species, sometimes identifying unique molt and stopover sites for different breeding populations (Ruegg et al. 2020, 2021, Rueda-Hernández et al. 2023). Integrating the resulting genoscapes with natural history data can reveal potentially causal associations between nonbreeding divergence and population structure. For instance, individual movement data, feather stable isotopes, and sequencing data from museum specimens recently revealed two genetically distinct clusters corresponding to a migratory and molt divide within the painted bunting *Passerina ciris* (Contina et al. 2013, Battey et al. 2018). It is likely that similar divides exist for other, less studied species, but have not yet been described. Although associations between nonbreeding adaptive variation and population structure can result from processes other than the former promoting the latter (Fig. 1), a potential causal relationship can be later tested through focused comparative studies or descriptions of hybrid phenotypes (below).

When does nonbreeding divergence overcome the homogenizing potential of migration?

The inherent potential of migration to facilitate gene flow may explain many instances of nonbreeding divergence existing in

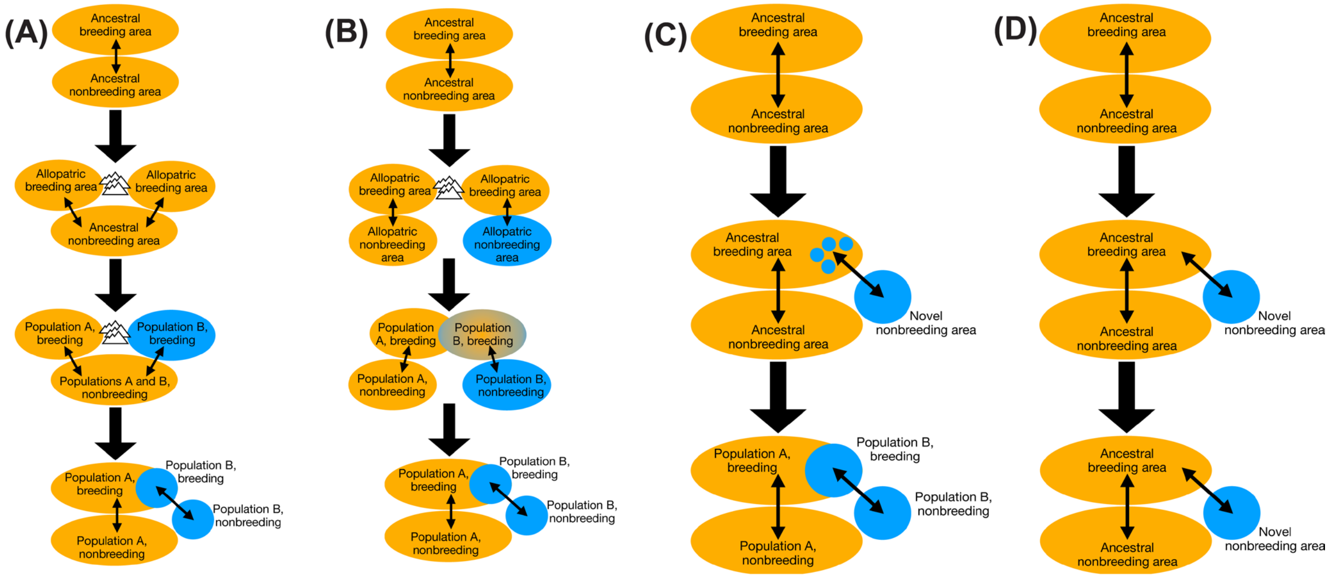

Figure 1. Three potential processes resulting in two species with different nonbreeding strategies: (A) nonbreeding adaptive divergence arises after complete reproductive isolation. (B) Diverging lineages evolve nonbreeding divergence during a period of allopatry. Following secondary contact, when reproductive isolation is incomplete and hybridization occurs, nonbreeding divergence propels speciation by manifesting as disadvantageous phenotypes in hybrids and in turn selecting for stronger prezygotic barriers. Scenario (C) is a proposed model of sympatric speciation via the evolution of novel nonbreeding strategies. In this scenario, some individuals begin spending nonbreeding periods in novel locations, potentially through vagrancy. Individuals with this novel strategy are more likely to mate with each other than individuals with the ancestral strategy, eventually becoming a novel species through primary divergence. Alternatively, in scenario (D), divergence in nonbreeding strategies arises but does not precipitate reproductive isolation.

the absence of strong reproductive isolation. What remains unclear, however, are the conditions required for nonbreeding adaptive divergence to impose reproductive isolation strong enough to outweigh the homogenizing effect of gene flow and drive speciation. Below, we identify some factors that may predictably determine whether or not nonbreeding divergence will result in speciation. Ultimately, testing these predictions requires comparisons of population structure and reproductive isolation between systems that differ with respect to these factors (Scordato et al. 2020) or phylogenetic comparative analyses testing the influence of these factors on diversification rates (Mason et al. 2017, Vinciguerra and Burns 2021).

Life history

Juvenile dispersal can homogenize lineages across wide geographic areas, potentially preventing fine-scale variation in selective pressures from promoting population structure and divergence. For example, while adult lesser yellowlegs *Tringa flavipes* exhibit variation in migratory routes and strong migratory connectivity, high juvenile dispersal maintains relatively low genetic differentiation across the species' range (Christie et al. 2023). Longer-lived species may be more likely to exhibit exploratory juvenile dispersal; because they have many opportunities to breed over their lifetimes, individuals may use their younger years to refine nonbreeding strategies that track resource availability patterns (Campioni et al. 2019). Therefore, we hypothesize that adaptive divergence in nonbreeding strategies may be less likely to promote speciation in longer-lived taxa.

Social behavior

When individuals pair with mates during nonbreeding periods, a behavior exhibited by many waterfowl and wading birds, individuals with similar nonbreeding strategies are more likely to interbreed with each other (Sonsthagen et al. 2024). Therefore, we predict that nonbreeding adaptive divergence may be more likely to promote reproductive isolation and propel speciation in lineages in which individuals select mates in nonbreeding areas.

The regulatory basis of nonbreeding strategies

The genetic architecture underlying nonbreeding phenotypes can have important implications for relative hybrid fitness, determining whether postzygotic reproductive isolation is strong enough to promote speciation in the face of gene flow. For instance, if coadapted trait complexes in parental populations break down in recombinant hybrid genomes, hybrids may exhibit intermediate or transgressive phenotypes, or combinations of traits from parental species (Lippman and Zamir 2007, Gompert and Buerkle 2016). These novel nonbreeding phenotypes may be strongly deleterious (Delmore and Irwin 2014, Dougherty 2023). Alternatively, selection for integrated migration, molt, and other nonbreeding strategies may cause the loci underlying these traits to occur in close proximity in the genome, possibly within inverted regions, such that they are inherited as a unit (Funk et al. 2021, Campagna and Toews 2022). In this scenario, hybrids would likely exhibit an intact nonbreeding strategy from either parental population, rather than combinations of traits (Abbott et al. 2013). The result may be polymorphism within a population, but not speciation. For instance, a large chromosomal inversion is associated with divergence in migratory strategy in common quail *Coturnix coturnix*. Individuals with the inversion are short-distance migrants or non-migratory, while individuals without the inversion are long-distance migrants. Heterokaryotypes display intermediate migratory phenotypes. Weak population genetic structure outside of the inverted region indicates extensive gene flow without significant reproductive isolation between birds exhibiting different strategies (Sanchez-Donoso et al. 2022).

How much does nonbreeding divergence really contribute to avian diversification?

More broadly, the fact that nonbreeding adaptive variation can exist without reproductive isolation may lead one to reason that nonbreeding divergence is not a widespread mode of speciation in birds. In this vein, many apparent associations between adaptive variation and population genetic structure or species boundaries could actually result from nonbreeding divergence arising incidentally after speciation has occurred, having made no meaningful contribution to the evolution or maintenance of reproductive isolation (Fig. 1). As outlined earlier in this review, several studies have identified systems in which nonbreeding divergence almost certainly imposes reproductive isolation between diverging lineages. However, is this scenario more common than nonbreeding divergence arising after complete reproductive isolation? Furthermore, if nonbreeding adaptive divergence is indeed a widespread mode of speciation in birds, at what stage of the speciation process is it most potent? We know through descriptions of hybrid phenotypes that nonbreeding divergence can impose reproductive isolation between diverging parental lineages following secondary contact, but is it also possible for novel nonbreeding adaptations to initiate reproductive isolation from a single ancestral population? To more accurately appreciate the contribution of nonbreeding adaptations to avian diversification, it is necessary to describe the evolution of both nonbreeding adaptive variation and reproductive isolation in a variety of systems.

Hybrid zones provide ornithologists with abundant opportunities to observe how nonbreeding adaptations influence reproduction at different stages of divergence (Harrison 1993, Dougherty and Carling 2024). While several studies have described migratory orientation in hybrids between populations with different migratory routes (Helbig 1991, Delmore and Irwin 2014), the potential for other types of nonbreeding divergence to influence hybrid phenotypes remains unclear. Moreover, extremely few studies have estimated the relative fitness of hybrid phenotypes in natural settings, where environmental factors may mediate the cost of endogenous incompatibilities or seemingly disadvantageous phenotypes (Thompson et al. 2022, Blain et al. 2024). For instance, supplemental food sources in human-altered landscapes may negate potential costs of inefficient aerobic metabolism or compromised cognition in hybrids (Grabenstein et al. 2023). Although describing phenotypes and quantifying the lifetime fitness of individual birds is not feasible in most systems, museum specimens (Peery et al. 2007), banding datasets (Specht and Arnold 2018), and photograph repositories (Hines et al. 2023) now enable ornithologists to easily compare age ratios among populations, ancestry classes, and over time. Comparing the relative proportions of adults and subadults between hybrid and unadmixed individuals is one way to test how hybrid phenotypes in systems with nonbreeding divergence in parental taxa influence survivorship (Rohwer et al. 2023). Additionally, by assuming detection to be a proxy for survival, tracking devices can sometimes reveal individual survival over time (Blain et al. 2024).

Previous studies of hybrid zones have demonstrated that nonbreeding divergence can maintain and strengthen reproductive isolation between parental populations following secondary contact (Turbek et al. 2017). However, a far less explored possibility is whether nonbreeding divergence can arise and promote speciation within a single ancestral breeding population via primary divergence. Although it is difficult to explore relationships between the evolution of nonbreeding adaptations and the evolution of reproductive isolation based on extant avian diversity, anthropogenic climate and landscape changes now present ornithologists with opportunities to observe these processes as they unfold. Human activity is rapidly altering selective pressures on nonbreeding strategies. Studies of long-term community science data have demonstrated that populations often vary in their responses to these pressures, introducing novel instraspecific nonbreeding variation (Youngflesh et al. 2023). Furthermore, nonbreeding divergence can arise within a single migratory population when a small proportion of individuals deviate from the population's typical routes, a phenomenon understood to occur annually in most migratory species (Diamond 1982). While most such 'mistakes likely lead birds to insufficient nonbreeding habitat, novel shifts in spatial and temporal distribution of resources may make some of these straying routes viable (Hill et al. 1998). Studies of Eurasian blackcaps *Sylvia atricapilla* have revealed perhaps the best described example of contemporary evolution in nonbreeding strategy. This species breeds broadly throughout Europe and historically overwintered predominantly in southern Europe and northern Africa. Beginning in the 1950s, however, increasing numbers have overwintered in the British Isles every year, likely enabled by supplemental winter feeding (Berthold and Terrill 1988). Studies of captive birds have demonstrated that this novel strategy has a strong genetic basis and is heritable (Berthold et al. 1992). Carry-over effects of migration on the rest of the annual cycle combined with different selective pressures in different nonbreeding areas appears to promote assortative mating between individuals with similar nonbreeding strategies, seemingly initiating reproductive isolation within a single breeding population (Bearhop et al. 2005). Genetic differentiation between individuals overwintering in Britain and individuals overwintering in ancestral areas in southern Europe supports this hypothesis (Rolshausen et al.

2009). Describing novel nonbreeding strategies as they arise in other systems (Hill et al. 1998) and mechanistically testing whether they are associated with the evolution of reproductive isolation may reveal that nonbreeding divergence frequently promotes reproductive isolation from sympatry.

Conclusion

Natural and sexual selection rarely act on individual phenotypes in isolation. Instead, selection favors the evolution of integrated adaptive complexes that enable individuals to track resources and minimize risk throughout the year. An historic focus on the breeding period has left abundant opportunities for studying how this adaptive variation in nonbreeding strategies influences reproductive isolation. Thankfully, identifying threats to birds during the entire annual cycle is now a primary objective in avian conservation, resulting in a wealth of individual tracking and year-round population genetic data. By using these rapidly growing datasets to test predictions at broader scales, ornithologists may be able to reconcile empirical work suggesting a causal role of nonbreeding divergence in speciation with contradictory population genetic studies. This future research has great potential to refine our understanding of the relative importance of nonbreeding adaptive varation in avian diversification.

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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