

Annual Review of Animal Biosciences Genetics and Evolution of Bird Migration

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Keywords

bird migration, genetics, evolution, migration strategy

Abstract

Bird migration has long been a subject of fascination for humankind and is a behavior that is both intricate and multifaceted. In recent years, advances in technology, particularly in the fields of genomics and animal tracking, have enabled significant progress in our understanding of this phenomenon. In this review, we provide an overview of the latest advancements in the genetics of bird migration, with a particular focus on genomics, and examine various factors that contribute to the evolution of this behavior, including climate change. Integration of research from the fields of genomics, ecology, and evolution can enhance our comprehension of the complex mechanisms involved in bird migration and inform conservation efforts in a rapidly changing world.

1. INTRODUCTION

Since the beginning of antiquity, the phenomenon of bird migration has long fascinated and impressed humankind, prompting a series of key questions about migratory birds: Where do they come from? Where do they go? How do they know the way home? The mystery of bird migration has given rise to many classic studies since the last century, which have explored various aspects of migration, including genetics, evolution, ecology, and conservation (1). Given length limits and our background knowledge, we focus primarily on advances in research on the genetics and evolution of bird migration. Nevertheless, we are fully aware that conducting a comprehensive review in this field is challenging, given the complexity of bird migration behavior (2, 3).

In the past decade, the progress of technology, much like in other fields, has greatly facilitated the development of science, and this is particularly evidenced by the research on the genetics and evolution of bird migration, mainly due to the revolutionary progress that has been achieved in genomics and tracking technology. In recent years, there has been a growing trend toward the use of whole-genome sequencing data in bird migration studies, ushering in the era of migration genomics (3). Additionally, technological advancements have made it possible to remotely track various animals over long distances at the individual level, thanks to the miniaturization and improvement of tracking technology (4, 5). These technologies have provided great support for characterizing and quantifying migration phenotypes and yielded abundant data for deeper investigations into the genetics and evolution of bird migration.

In this context, we aim to present an overview of recent advances in genetics and evolutionary research related to bird migration, based mainly on several classical migration systems. We also discuss various factors that influence the evolution of bird migration, such as climate change, and highlight promising directions and challenges that need to be addressed in future.

2. MIGRATION: AN EVOLVED COMPLEX BEHAVIOR IN BIRDS

In this review, we adopt the definition of migration as outlined by Liedvogel (6), which refers to the seasonal mass movements of all or a fraction of individuals belonging to a particular group (that group may be a species, subspecies, or population) of animals from one region to another in a coordinated and direct manner. It is important to note that this definition excludes altitudinal migration and dispersal.

Migration is an evolutionary behavior driven by seasonal changes in environmental resource availability. This is due to the tilted axis of the Earth's rotation, resulting in seasonal variation in solar radiation received by the two hemispheres on either side of the equatorial plane, with the greatest degree of variation occurring closer to the poles. As a result, birds living at high latitudes with strong seasonal variation in environmental resources commonly migrate to middle or low latitudes to avoid disadvantageous living conditions (7). From an evolutionary perspective, migration can be seen as an adaptive strategy for birds to survive in areas with strong seasonal variations in environmental resources. Conversely, birds living in regions with less seasonal variation choose not to migrate because the benefits may not outweigh the costs in terms of time, energy, and survival (8–11).

At the same time, migration is a complex behavior influenced by the rich diversity of avian species and their specific requirements. Factors driving this adaptive behavior differ among bird species, including spatiotemporal distributions of resources, habitats, predation, and competition (12). One notable aspect of these complexities is their high degree of flexibility, which enables them to change rapidly. For example, the Eurasian blackcap (*Sylvia atricapilla*) developed new migration routes in just a few generations (13), house finches (*Haemorhous mexicanus*) quickly developed migration behavior after their introduction to North America (14), and whooping

cranes (*Grus americana*) can quickly learn to migrate through human training (15). Recently, a new migratory route for pink-footed goose (*Anser brachyrbynchus*) on Novaya Zemlya, Russia, was reported to be related to cultural transmission from taiga bean geese (*Anser fabalis*) (16). These examples illustrate the complexity of bird migration and the challenges involved in studying the genetics and evolution of this behavior.

Despite the complexity of bird migration, over the past few decades, significant progress has been made in understanding its genetic programming and evolutionary origins and in identifying potential genetic loci relevant to migration behavior. These achievements resulted largely from the establishment of some classical bird migration research systems (**Figure 1**). Examples of model species used in migration research systems include the European starling (*Sturnus vulgaris*), Eurasian blackcap, willow warbler (*Phylloscopus trochilus*), and Swainson's thrush (*Catharus ustulatus*), as well as new systems that have emerged with advances in genomics and tracking technology. Although these systems differ in terms of geographic coverage, taxonomic groups, and migration strategies, they complement each other and contribute to our understanding of migration in general. Here, we review the scientific history, migration questions, and major research outcomes of these research systems.

2.1. European Starlings

Perdeck (17) used European starlings mainly for large-scale displacement experiments. European starlings are widely distributed, but the breeding population in northern Sweden is migratory, and these birds travel in a southwestern direction along the western coast of the Netherlands in autumn each year. Perdeck (17) conducted a series of large-scale displacement experiments from 1948 to 1957, which involved translocating more than 10,000 starlings (adults and juveniles) from the Netherlands to Switzerland. Analysis of ring recovery data showed that the adult starlings had a true goal orientation, meaning they aimed toward their original wintering area in a northwest direction. However, the juvenile starlings flew in a direction similar to the preferred direction, indicating a one-direction orientation. Thus, Perdeck concluded that during autumn migration, adult starlings use a homing orientation, whereas juveniles use a one-direction orientation (17, 18).

2.2. Eurasian Blackcaps

The Eurasian blackcap migration system represents one of the most extensively studied systems of bird migration to date. The blackcap is a common species occurring throughout Europe, exhibiting a wide range of behavioral variations in its migratory habits (e.g., propensity to migrate, timing, and direction). Much understanding about bird migration genetics and evolution has been gained in this species. Early ring recovery experiments (19, 20) revealed the presence of populations that either did not migrate at all or migrated in autumn to different orientations (northwest, southwest, or southeast). In 1981, Berthold & Querner (21) conducted hybridization experiments on Eurasian blackcap populations that were either fully migratory or only partially migratory. They found that the hybrid blackcaps exhibited intermediate migratory restlessness, demonstrating that the genetic basis of migratory distance exists in this avian species. Further studies through crossbreeding and common garden experiments found that the migratory direction of blackcaps is genetically controlled, as hybrid blackcaps display intermediate migration direction (22, 23). In summary, studies on the Eurasian blackcap system have contributed significantly to our understanding of the genetics of migratory behavior in birds.

2.3. Willow Warblers

Similar to the Eurasian blackcap, the willow warbler also exhibits diverse migration strategies and has been a focal species for the studies of migration genetics for more than 20 years (24–29). The



Figure 1

Representative avian species for bird migration research. Five representative research systems: (*a*) Eurasian blackcaps, (*b*) willow warblers, (*c*) Swainson's thrushes (ML590680861), (*d*) golden-winged warblers (ML589976421) and blue-winged warblers (ML583813531), and (*e*) peregrine falcons. Bird photographs in panels *c* and *d* adapted with permission from the Macaulay Library at the Cornell Lab of Ornithology. Migration routes are illustrated based on published studies (36, 38, 44, 47, 55).

willow warbler is a small, long-distance migratory songbird that breeds in the northern parts of the Palearctic from western Europe to eastern Siberia (30); it includes three subspecies: *Phylloscopus trochilus trochilus, P. trochilus acredula*, and *P. trochilus yakutensis*. The subspecies *P. trochilus trochilus* breeding in western Europe migrates southwest to wintering areas in West Africa, whereas *P. trochilus acredula* breeding in northern and eastern Europe migrates southeast to wintering areas in eastern and southern Africa (31–33). Despite the two subspecies showing almost no genetic differentiation in mitochondrial DNA and microsatellite markers (24), they likely diverged during the end of the Pleistocene or early Holocene and colonized Scandinavia from different directions: *P. trochilus trochilus* from the south and *P. trochilus acredula* from the east of the Baltic Sea via Finland (26). The narrow hybrid zone between the subspecies in Central Sweden is thought to be maintained by selection against an intermediate migratory program in the hybrids (26). To gain a deeper understanding of the migratory system of the willow warbler, additional studies using various methods, such as amplified fragment length polymorphism (AFLP), candidate-gene, and whole-genome mapping (2, 34–36), were conducted to investigate the genetic architecture underlying migration direction (see Section 3.1).

2.4. Swainson's Thrushes

The three aforementioned research systems are concentrated primarily along the African-Eurasian migration flyway. In North America, researchers established a research system using Swainson's thrush as the study subject to investigate the genetic basis of migration route variations (e.g., 37, 38). Swainson's thrush, a small, long-distance migratory bird, comprises two subspecies groups, with the coastal group of the North American Pacific Coast migrating along the western flank of the Rocky Mountains, southward to Mexico and Central America, and the continental group migrating from the eastern side of the Rocky Mountains to their wintering grounds in South America (39). Subsequent studies provided more detailed information about their migration routes using light-level geolocators (40). To test the intermediate route hypothesis, Delmore & Irwin (37) tracked 15 hybrids between the coastal and continental populations of the Swainson's thrush and found that approximately half of the hybrids displayed an intermediate migratory behavior, providing the strongest evidence for the intermediate route hypothesis so far. Following this, whole-genome sequencing was performed, and the most significant genetic differences were identified on a specific region of chromosome 4 between the two subspecies. This region, including circadian, nervous system, and cell signaling genes, was found to be under selection and strongly associated with migratory orientation (38).

2.5. Other Migration Systems

Recently, a few more avian species [e.g., yellow warbler (*Setophaga petechia*) (41, 42), red-backed shrike (*Lanius collurio*) (43)] have been studied by incorporating new tracking technologies [e.g., geolocators and GPS (global positioning system)] and genome-wide sequences to address scientific questions related to, e.g., the genetic basis of migration behavior and the influence of climate change on bird migration. For example, at the species level, Toews et al. (44) conducted genome sequencing on golden-winged warblers (*Vermivora chrysoptera*) and blue-winged warblers (*Vermivora chrysoptera*), which have distinct wintering grounds (45, 46) in Central and South America, to investigate the genetic effects of varying migration and wintering grounds. At the population level, Gu et al. (47) employed satellite tracking and population genomic sequencing on peregrine falcons (*Falco peregrinus*) distributed in the Arctic of Eurasia to explore the genetic basis for different migration distances.

3. GENETICS OF BIRD MIGRATION

In the late twentieth century, several studies demonstrated that migratory behavior in birds is genetically determined, primarily through the use of displacement and selective/cross-breeding experiments in established study systems [e.g., Eurasian blackcaps (21)]. Subsequently, studies using quantitative genetics methods have estimated the heritability of migratory traits in birds (48) and have also compared the differences in heritability between traits closely related to bird migration behavior (e.g., migratory timing and direction) and other traits (e.g., wing length). Generally, migratory traits have lower heritability (migratory activity: 0.37-0.45; timing of autumn migration: 0.34–0.45) than morphological traits (wing length: 0.67–0.73) (48). This is in agreement with the observation that traits more closely related to fitness tend to have lower heritability and higher variation (2). Additionally, many studies have shown that migratory traits are correlated for instance, migratory timing potentially affects molt timing (49) and breeding time (50)-further highlighting the complexity of migratory behavior. As a result, scientists have begun to define the genetic architecture of migratory traits as a "migratory gene package" (51, 52) or "migratory syndrome" (53, 54). Since the 1990s, the emergence of molecular genetics has enabled researchers to use marker-based approaches (e.g., AFLP) and candidate-gene analysis to study the genetic architecture of migratory traits, laying a foundation for later genomics research. In the past decade, with the development of cutting-edge technologies such as genomics and transcriptomics, researchers have shifted from studying migratory genetics to migratory genomics (3) and have begun to explore the epigenetics and functional genomic foundation for migration (55).

Birds that can successfully complete migration not only require navigation skills (56) but also need to depart at appropriate times and in the correct direction, spend winter at a suitable location (**Figure 1**), and be well-prepared in terms of morphology (e.g., molt) and physiology (e.g., fat deposition). Therefore, in this section, we focus primarily on the progress of three aspects of bird migration genetics: behavioral, morphological, and physiological.

3.1. Genetic Basis of Migration Timing, Direction and Distance

Migration is a highly complex behavior influenced by a multitude of factors. Exploring the genetic basis of migration in a behavioral aspect provides captivating insights into these intricate mechanisms. Below we review published studies that illuminate the genetic basis of migration, focusing on three fundamental components that depict the migration behavior: timing, direction, and distance.

3.1.1. Timing. One of the main decisions that birds face during the onset of migration is determining the appropriate time to depart and, at the end of their journey, when to stop (**Figure 2***a*). Generally, the timing of migration can vary across species, populations, and even individuals within a population, mainly due to their internal clock mechanism (57). Nonetheless, external factors, such as photoperiod, can also play a role in influencing the urge to migrate, as observed in both artificially captive and wild migratory birds (58). This migratory restlessness, often referred to using the German term *Zugunrube*, reflects the innate clock birds have to initiate their migration and was widely used as a proxy for migration timing and distance in early studies (21). Recently, genetic research on bird migration timing has turned to using the candidate-gene approach, mainly examining the polymorphism of genes relevant to rhythm clock activity previously identified in model organisms (59). These studies aim to correlate gene polymorphism with migratory phenotypic variation (e.g., migration timing, latitude clines, breeding and molting times) among different species or populations.

Among the candidate genes that have been tested for potential association with migration time (e.g., *Clock, Adcyap1, CREB1*), *Clock* is the most extensively studied, but many conclusions remain



Figure 2

Behavioral differences, main genetic basis, and evolution for bird migration. (*a*) Main behavioral differences in migratory timing, direction, and distance. (*b*) Genetic basis of behavioral difference. Three representative gene sets related to migration strategies are illustrated. For the *Clock* gene, variations in the length of a glutamine repeat have been linked to migration timing. The figure shows three genotypes of InvP-Ch1 (Acr, homozygote for *acredula* allele; Het, heterozygote; Tro, homozygote for *trochilus* allele) in combination with the presence (1) or absence (0) of the fragment MARB-a (36). Whereas the combination of InvP-Ch1 and MARB-a explains 74% of variation in autumn migration direction, MARB-a alone can explain 62%. Two haplotypes of the *ADCY8* gene are shown (47). SD and LD indicate short-distance and long-distance migrants, respectively. (*c*) Evolution of bird migration from the Early Eocene to the present and near future is illustrated with maps adapted from the PaleoAtlas project (143). The figure also shows possible migration strategy changes that birds may take under climate change (e.g., shortened migration distance, formation of new migration route). Panel *b* (*middle and right*) adapted with permission from References 36 and 47, respectively.

controversial. *Clock* is associated with the circadian clock activity rhythm found initially in mice (59). Toward the 3' end of the gene, there is a polyglutamine (poly-Q) repeat region that can vary in length among and within species, resulting in shorter and longer alleles (**Figure 2b**). Johnsen et al. (60) conducted the first investigation of *Clock* polymorphisms in avian populations, finding that in the 13 populations of blue tits (*Cyanistes caeruleus*), *Clock* length was correlated with the clinal latitude of their habitats. Later, Liedvogel et al. (61) found a significant correlation

between *Clock* gene variations and breeding timing within the same species. Further studies of *Clock* gene polymorphisms in birds have revealed significant associations with other migratory phenotypes, such as propensity to migrate (62), migratory schedule (63, 64), and timing of molt (65). In contrast, many other studies could detect no significant correlation between *Clock* polymorphism and migratory behavior or geographic location in birds (66–70). Given the inconsistent results within and between different taxa, the role of the *Clock* gene in migration timing of birds remains uncertain (28, 55).

Le Clercq et al. (71) recently conducted a systematic review of all previously published studies examining the relationship between polymorphisms in five candidate clock genes (*Clock, Adcyap1*, *CREB1, NPAS, DRD4*) and seasonality in a phylogenetically and taxonomically informed manner. They analyzed candidate-gene polymorphisms in 76 bird species (58 migrants and 18 residents) and population genetic data for 40 species. They provided evidence of a putative association between *Clock* gene variation and autumn migration, as well as between *Adcyap1* gene variation and spring migratory from sedentary birds, in line with previous results based on 70 bird species (72). Nonetheless, they found correlated variability in both genes with divergence time, indicating a potential for ancestrally inherited genotypes to influence contemporary changes driven by selection (71). These studies again suggest a tentative association between these candidate genes and migration attributes as well as genetic constraints on evolutionary adaptation (71).

3.1.2. Direction. The genetic basis of migration direction has been a main focus in the field of migratory behavior genetics (**Figure 2***a*). Early classic experiments were conducted predominantly using Eurasian blackcaps. For instance, a study using experimentally crossbred blackcaps from populations with southwest and southeast migration demonstrated that F1 hybrids exhibited an intermediate direction toward the south (tested in Emlen funnels) (22), leading to the so-called intermediate route hypothesis (22, 23). However, these experiments were conducted mainly in orientation cages and may not truly represent actual orientation in the wild.

In the wild, closely related species or neighboring populations within a species may have different migratory directions, and their hybridization in the overlapping distribution area forms a contact or hybrid zone. This natural crossbreeding experiment can be used to test the inheritance pattern of migratory direction. After the crossbreeding experiments on blackcaps, some attempts were made to investigate the orientation of hybrids between pied flycatchers (*Ficedula hypoleuca*) and collared flycatchers (*Ficedula albicollis*) and between great reed warblers (*Acrocephalus arundinaceus*) and clamorous reed warblers (*Acrocephalus stentoreus*) in the wild, using stable isotope analyses of feathers molted at the wintering grounds (73–75). However, in contrast to the observations on blackcaps (22), these studies found that interspecific hybrids may migrate similarly to one of the two parental species, reflecting the dominance of genetic determinants, with intermediate characteristics showing only an additive effect. However, due to the low precision when predicting molting areas of individual birds using the stable isotope method, these results should be further validated using more accurate positioning technologies, such as GPS tracking.

In Swainson's thrushes, Delmore & Irwin (37) provided the first direct test of the intermediate route hypothesis in the wild using light-level geolocator methods. They found that hybrids of Swainson's thrushes exhibited increased variability in their migratory routes compared to their parents, with some using intermediate routes and some using the same routes as one parental group on fall migration and the other on spring migration (37). In addition, hybrids also tended to use geographically intermediate wintering sites. They also analyzed the genetic variation across the hybrid zone and suggested that hybrids were affected by moderately strong selection, which may play a role in speciation (37). Furthermore, they also identified an \sim 30-Mb block on chromosome

4 containing a cluster of single-nucleotide polymorphisms (SNPs) that was putatively associated with migratory direction in Swainson's thrushes tracked with geolocators and in a separate group tested in captivity (38). Beyond these, Toews et al. (44) conducted a comparative genomic analysis between migratory golden-winged and blue-winged warblers that have the same breeding ground but different wintering areas and found a single locus correlating with different winter longitudes, a gene coding for vacuolar protein sorting 13A (*VPS13A*).

In the willow warbler, several key questions about migration directions have been answered recently (34-36). As mentioned above, the subspecies P. trochilus trochilus breeds in western Europe and migrates toward southwestern to western Africa, whereas the subspecies P. trochilus acredula breeds in northern and eastern Europe and migrates southeast to eastern and southern Africa. Although early studies using mitochondrial DNA and microsatellite data found little genetic differentiation between these two subspecies, despite differences in their migratory directions (25). a vast majority of highly differentiated variants found between the two subspecies were located in regions of chromosomes 1 and 5 based on whole-genome sequencing and a customized SNP array (29). Furthermore, Caballero-López et al. (35) found that two previously identified (26) variants of a WW2 AFLP marker (WW2-ancestral and WW2-derived) were located in a long terminal repeat sequence of a transposon. Specifically, the WW2-derived variant shows a higher copy number in the *P. trochilus acredula* subspecies and is present in a repeat-rich region (MARB-a) (35). Although this region was not located in the highly differentiated regions previously identified on chromosome 1 or 5 (29), the element may interact with genes regulating migratory direction (35). In addition, a recent investigation using an integrative approach involving sequencing long reads, linked reads, and optical mapping has uncovered the existence of two chromosomal inversion regions located on chromosomes 1 and 5 (InvP-Ch1 and InvP-Ch5), respectively (34). Sokolovskis et al. (36) observed that allele frequencies at these genetic loci (InvP-Ch1, InvP-Ch5, and MARB-a) exhibited geographic clines that coincided with changes in migration direction and hypothesized that these loci contain, or are situated near, genes encoding various migratory strategies. To test it, they tagged individuals from the two subspecies in northern and southern Sweden, respectively, to establish migratory phenotypes of allopatric subspecies and deployed 356 geolocators at the Scandinavian migratory divide (36). For each individual, they genotyped for InvP-Ch1. InvP-Ch5, and presence or absence of MARB-a. They found that the P. trochilus trochilus allele at InvP-Ch1 is associated with a dominant effect for southwestern migratory direction, whereas the repeat-rich region (MARB-a) is associated with a dominant effect for southeastern migratory direction (36). Moreover, they also found that 74% of the variation in migration direction of willow warblers was explained by a combination of MARB-a and InvP-Ch1, both with a dominant inheritance pattern and MARB-a suppressing InvP-Ch1 through epistasis (Figure 2b). As a consequence, most hybrids are expected to migrate similarly to one of the parental subspecies and therefore do not suffer from the cost of following an intermediate route (36). This is consistent with hybrids of pied and collared flycatchers (73) but contrasts with the codominantly determined patterns observed in Eurasian blackcaps (22, 76) and Swainson's thrushes (37, 38), where F1 hybrids expressed intermediate orientations relative to parental forms.

In addition to passerines, Väli et al. (77) used GPS telemetry to compare the autumn journeys and wintering ranges of two closely related large raptorial bird species, the greater spotted eagle (*Clanga clanga*) and the lesser spotted eagle (*Clanga pomarina*), and hybrids between them. They found that the timing of migration in hybrids was similar to that of *C. pomarina*, but the wintering distributions and home range sizes were similar to those of *C. clanga*. These results suggested that, although the contribution of social interactions cannot be ruled out, a strong genetic component seems to be involved in the evolution of migration strategy in the raptorial species via a traitdependent dominance effect (77). To date, several independent studies have endeavored to identify genomic regions associated with differences in migration direction: Delmore et al. (38) with Swainson's thrushes, Toews et al. (44) with golden- and blue-winged warblers, Delmore et al. (76) with Eurasian blackcaps, and studies with willow warblers (2, 34–36). However, none of the identified genes were shared, as reported by Delmore et al. (76) and Sokolovskis et al. (36), raising doubts about the existence of a common genetic basis for bird migration orientation across taxonomic groups (3, 36, 76).

3.1.3. Distance. Migratory birds face additional challenges in determining suitable wintering sites or the distances they need to travel before coming to a halt (**Figure 2***a*). Similar to migration time and direction, migration distance also exhibits variations among different species and among populations within species. Notably, the Arctic tern (*Sterna paradisaea*) holds the record for the longest recorded migration distance, annually covering a round-trip distance of up to 80,000 km between the Arctic and Antarctic (78). Long-distance migration imposes greater demands on birds' abilities to navigate and orientate their flight (79). Here we summarize advances in this research area in two main aspects: the measurement using migratory restlessness and the genetic basis using candidate genes or genome approaches.

Historically, research on migratory distance was depicted indirectly via the duration of migratory activity (e.g., migratory restlessness). Studies conducted on several bird species, such as willow warblers, chiffchaffs (*Phylloscopus collybita*), Eurasian blackcaps, and garden warblers, under similar and constant conditions, indicated that long-distance migrants exhibited more migratory activities than their middle-distance counterparts (58, 80, 81). Quantitative comparisons of the nocturnal restlessness of caged experimental birds also aligned well with the migratory behavior of free-living conspecifics (58, 80, 81). Further evidence (82) supporting this hypothesis came from the contrasting behavior of six *Sylvia* species of different migratory habits, ranging from the long-distance migratory garden warblers to the almost sedentary Marmora's warblers (*Sylvia sarda*). Researchers also scored migratory activities in captive birds and compared the behavior of sedentary and migratory blackcaps and their hybrid offspring (21); results indicated that the duration of migratory activity is a quantitative multi-locus trait (83). Overall, the duration of migratory activity is actually a useful proxy for estimating total migration time (in proportion to migration distance), particularly in the absence of tracking technology.

Early on, candidate-gene-based approaches were used mainly to investigate the genetic basis of migratory distance. For instance, Mueller et al. (69) studied polymorphisms in the exons of six candidate genes in blackcaps and found a consistent association between microsatellite polymorphism and migratory distance in the Adcyap1 gene. However, Peterson et al. (62) found no consistent relationship across all congeneric species for Adcyap1 or Clock length polymorphisms and phenological traits. They only found longer Clock alleles in two subspecies that migrate longer distances and a relationship between Adcyap1 length and migratory restlessness in one of the two captive populations (62). In a comparative study of 23 trans-Saharan migratory bird species. Bazzi et al. (84) investigated the relationship between species-level genetic variations at *Clock* and Adcyap1 and species traits related to migration and geographic distribution. They found that Clock allele size increased with breeding latitude across species and that species migrating over longer distances had significantly reduced *Clock* (but not *Adcyap1*) gene diversity. By using a phylogenetic confirmatory path analysis, they suggested that migration date and distance were the most important variables directly affecting Clock gene diversity (84). In contrast, studies on a neotropical migratory passerine, the painted bunting (Passerina ciris), found no correlation between the size of microsatellite alleles of Adcyap1 and Clock genes and migration onset or duration (64). Recently, de Almeida Miranda et al. (85) tested for correlations between astrocyte morphological complexity, migratory distances, and the size of the Adcyap1 allele in three long-distance migrant species

of shorebirds and one sedentary species. They found significant associations between the size of the *Adcyap1* microsatellites, migratory distances, and the degree of morphological complexity of astrocytes. They suggest that polymorphism in the gene *Adcyap1* may underlie variations in the migratory phenotype and that both the size of the *Adcyap1* allele and astrocyte morphological complexity are strongly related to migratory distances. But there are some limitations when studying migration genetics in shorebirds, such as ranges restricted to narrow strips along the coasts of continents, as Le Clercq et al. (71) recently pointed out. In this recent review, Le Clercq et al. (71) conducted a systematically phylogenetic generalized least squares analysis using all available data but found no significant relationships between the average latitudes of breeding and nonbreeding ranges and the allele length of the most common *Clock* or *Adcyap1* alleles. The only significant relationship was observed between *Clock* allele length and total migration distance (71).

To date, only a few studies have used whole-genome sequences to investigate the genetic basis of migratory distance, but they have already revolutionized the field. Delmore et al. (76) conducted a genome-wide association study (GWAS) on Eurasian blackcaps, quantifying migratory distance as an ordinal variable from short- to medium- to long-distance migrants. A significant proportion of variances in migratory distance could be explained by their set of SNPs, with one SNP at the downstream of the KCNIP1 gene showing a strong association with migratory distance. KCNIP1 encodes a potassium channel-interacting protein, which functions in neuronal cell excitability. Given that migratory distance is a continuous variable, the authors also noted that directly quantifying migratory distance (e.g., geolocator) rather than using an ordinal variable to measure behavior of migrants could improve the analysis (76). At the population level, Gu et al. (47) integrated satellite telemetry tracking and whole-genome sequencing to investigate the genetic basis of long-distance migration in peregrine falcons. In their study, they found a connection between the gene ADCY8 and population-level variations in migratory distance (Figure 2b). The ADCY8 gene encodes adenylyl cyclase type 8, which plays a role in the conversion of ATP to cAMP and is known for its involvement in long-term memory (86, 87). Notably, the dominant ADCY8 genotype was observed in long-distance migratory peregrine populations, suggesting that longterm memory is the most likely selective agent driving divergence in ADCY8 among the peregrine populations (47).

3.2. Genes Associated with Migratory Morphology and Physiology

Migratory birds have also undergone adaptive changes in their morphology to enable them to undertake long-distance flights. One key migration-associated morphological change is feather molting: the replacement of older feathers by newer, more aerodynamic feathers before or during migration (88–91), which allows for increased flight efficiency (92). In partial migrant populations, migrants often suspend molt during autumn migration and resume in the wintering area (e.g., migratory peregrines). Previous studies have demonstrated that intraspecific variation in molt timing and location in birds is at least partially genetically determined in Eurasian blackcaps (21, 93), African stonechats (*Saxicola torquatus*), and European stonechats (*Saxicola torquatus rubicola*) (94), though few studies have looked at the genes involved in feather molting. Contina et al. (95) recently investigated the genetic basis of feather molting and the specific environmental drivers in painted buntings by integrating genome sequencing with stable isotope analyses. Molting was found to be regulated in part by two genes, *GLI2* and *CSPG4*, which link to feather development and structure (96, 97). Interestingly, genetic variations in these genes are associated with seasonal variation in precipitation and aridity, again suggesting that they may be related to migratory molting (95).

Another important aspect of migratory morphology is wing shape. Previous studies suggested that wing shape is heritable, and long-distance migrants tend to have longer or more pointed wings

than short-distance and nonmigratory birds (98, 99). Using a QTL (quantitative trait locus) scan, Tarka et al. (100) identified a single QTL that explains 37% of the variation in wing length in great reed warblers (*A. arundinaceus*). Schielzeth et al. (101) also reported six genomic regions linked to wing length variation in captive zebra finches (*Taeniopygia guttata*). However, when performing a GWAS analysis of restriction site–associated DNA sequencing data, again in great reed warblers, no significant association was detected (102). Taken together, these studies demonstrate that the genetic basis of wing morphology for bird migration is not yet fully understood, despite the trait's high heritability.

In addition to morphological changes, migratory birds also feature physiological changes, such as hyperphagia and alterations in fat metabolism, that enable them to undertake long-distance flights (103). Although the importance of physiology in bird migration has been reviewed extensively (79, 104), far fewer studies investigate the genetic basis for these physiological changes. Previous research has identified several genes related to muscle size (e.g., *IGF1*) in captive European starlings (105), as well as those involved in oxidative and catabolic pathways (e.g., *PPARa*, *PGC-1a*, *PGC-1β*, *ERRβ*, *FABPpm*, *Plin3*) and fatty acid oxidation (e.g., *LPL*, *MCAD*, *ATGL*) in gray catbirds (*Dumetella carolinensis*) (106). A recent review (107) highlighted the behavioral and physiological capabilities that support extreme trans-Pacific flights of migratory shorebirds and emphasized the unique opportunities provided by the vastness and complex aeroscape of the Pacific Basin for studying the physiological capabilities of migratory birds. This sheds light on the genetic mechanisms underlying physiological adaptations in long-distance migration.

As stated above, using candidate-gene or genome approaches, past studies have identified a variety of genes associated with different migratory traits. However, the molecular mechanisms underlying bird migration are intricate and diverse, varying depending on specific traits or annual cycles [see a recent review by Sharma et al. (108)]. For example, when considering migration timing, internal factors like innate clock mechanisms are involved in initiating migration, whereas external factors such as photoperiod can also influence the urge to migrate. Genetic investigations into migration timing have focused primarily on the genes that regulate circadian rhythms, with *Clock* being studied extensively. Nonetheless, *Clock*'s role in migration timing remains to be explored due to inconsistent evidence reported previously, emphasizing the need for further research with more interdisciplinary approaches and controlled experimental conditions to gain a comprehensive understanding of its molecular mechanism.

3.3. Transcriptomic and Epigenetic Modifications and Their Role in Migratory Patterns

The molecular basis of migration behavior in birds is multifaceted and has both genetic and epigenetic components. Although more and more genetic loci have been identified to play a role during bird migration, recent research has begun to appreciate the role of epigenetic components in regulating migration behavior (55).

Transcriptomic studies using high-throughput sequencing techniques such as RNA-seq have contributed to our understanding of the genetic mechanisms involved in migratory behavior in birds. By comparing gene expression changes in blood samples between migratory and sedentary European blackbirds (*Turdus merula*), Franchini et al. (109) identified four differentially expressed genes associated with hyperphagia, molting, DNA replication, and transcription. Additionally, other transcriptomic investigations have focused on genes differentially expressed in other tissues, such as the brain (110, 111), heart, and liver (112, 113). For example, Frias-Soler et al. (110) used RNA-seq data to explore the biological functions associated with the seasonal brain signatures of the northern wheatear (*Oenanthe oenanthe*), identifying 84 differentially expressed genes related to nervous tissue development, angiogenesis, ATP production, innate immune response, and

antioxidant protection. These findings expanded our knowledge of the molecular processes underlying migratory behavior in birds.

Along with gene expression, epigenetic modifications like DNA methylation have also been linked to migratory behavior in birds. However, our understanding of the role of epigenetic modifications in avian migration is limited. Recent studies have identified candidate genes that may affect migratory phenotypes triggered by seasonal stimuli (55). For example, *Clock* has been linked to phenology (114), whereas *Mettl25* and *Acss3* have been associated with nocturnal flight (115). Saino et al. (114) investigated whether CpG methylation at the poly-Q and 5' untranslated region loci of the *Clock* gene predict migratory and breeding phenology in barn swallows (*Hirundo rustica*) and found that increased methylation at *Clock* poly-Q loci was associated with earlier spring departure from the African wintering area, arrival date at the European breeding site, and earlier breeding date. Such findings suggest that epigenetic modifications may have enduring effects on gene expression of the candidate gene, although these associations require further research to fully comprehend the complex relationship between DNA methylation and migratory pathways.

Overall, both transcriptomic and epigenetic studies are valuable for understanding the molecular mechanisms involved in migratory behavior (55). Given the complexity of bird migration, they also have limitations. Transcriptomic studies can generate lengthy candidate lists but may not have the means to perform further functional tests. On the other hand, epigenetic studies have important implications for understanding migratory behavioral changes in birds due to their high sensitivity, but they also further highlight the complexity of bird migration.

4. EVOLUTION OF BIRD MIGRATION

Approximately 19% of avian species worldwide exhibit migratory behavior, which plays a pivotal role in regulating global biodiversity (116). The reasons why birds migrate are complex. Previous studies suggested that the proximate factors include ecological and physiological determinants, whereas ultimate factors encompass evolutionary history and other factors. In addition, growing evidence demonstrates that bird migration behavior can change rapidly, which has significant implications in the context of global climate change. In this section, we review recent research advancements regarding benefits and costs of avian migration, evolutionary history, and the role of environmental change in shaping the evolution of bird migration.

4.1. Benefits and Costs of Bird Migration

Migration is widely recognized as an adaptive strategy that enhances individual fitness and is subject to natural selection. By moving across different regions for breeding or wintering, birds can obtain a variety of benefits, including but not limited to greater access to food resources (117), avoidance of predators (118), and reduction of intra- or inter-specific competition (119).

The benefits of migration in birds are influenced not only by the decision to migrate but also by the specific migration strategies employed. Winger & Pegan (120) investigated the relationship between migration distance and the trade-off between reproduction and survival in 45 passerine bird species that breed in North American boreal forests and migrate to various winter environments and latitudes. They found that longer-distance migrations to more favorable winter environments were associated with lower annual reproductive output but higher adult survival rates than shorter-distance migrants, even after controlling for mass and phylogeny.

Despite obvious benefits of migration, costs associated with this behavior can impact the survival and reproductive schedules of migratory species. Direct evidence on the timing and location of migrant mortality has been provided by identifying cases of confirmed and probable threats in three long-distance migratory raptorial species tracked by satellite telemetry (9). The study found that mortality rates were approximately six times higher during migration seasons than during stationary periods (breeding or wintering), indicating that events during migration have a substantial impact on the population dynamics of long-distance migrants (9). Similarly, Rockwell et al. (121) demonstrated recently that migration is the season of highest mortality in Kirtland's warblers (*Setophaga kirtlandii*).

The costs associated with migration can also vary depending on the migratory strategy employed. For instance, Lok et al. (122) compared the seasonal survival of Eurasian spoonbills (*Platalea leucorodia*) that breed in the Netherlands and migrate different distances (ca. 1,000, 2,000, and 4,500 km) to winter in France, Iberia, and Mauritania, respectively. Whereas summer, autumn, and winter survival were high and independent of migration distance, mortality during spring migration was significantly higher (18%) for birds that wintered in Mauritania than for those that flew only as far as France (5%) or Iberia (6%). Higher mortality during long migration likely was driven by the presence of a physical barrier (the Sahara Desert) in combination with suboptimal fueling and unfavorable weather conditions en route (122). Hewson et al. (123) observed similar phenomena in the common cuckoo (*Cuculus canorus*) population in the United Kingdom. Mortality up to the completion of the Sahara crossing is higher for birds using the shorter route, which correlates strongly with population decline across nine local breeding populations (123). These findings highlight the importance of considering the costs and risks associated with different migratory strategies when studying population dynamics and conserving migratory species.

4.2. Evolutionary History of Bird Migration

The imprint of past evolutionary forces could be considered one of the ultimate causations for bird migration. From an ecological perspective, migratory birds should follow the most optimal migration routes. However, many species exhibit migration patterns that do not align with ecological efficiency but rather reflect the migratory paths of their ancestors. The northern wheatear is a noteworthy example. Originally inhabiting Eurasia, wheatear populations from Siberia expanded eastward to colonize Alaska following the deglaciation of northern ice sheets after the Last Glacial Maximum, whereas wheatears from Europe moved westward across Greenland to breed in the Canadian High Arctic. Despite their current distribution on either side of North America, all northern wheatear populations continue to follow their ancestral migratory paths to winter in sub-Saharan Africa, as confirmed by geolocator tracking (124). These findings underscore the constraining influence of evolutionary change as a driving force in bird migration.

The evolution of bird migration is widely accepted to have occurred early in the evolutionary history of avian species and is observed across all groups (51, 125). What remains controversial are the history (which state was ancestral?) and geographic origins (the tropics or the temperate region?) of these transitions (126). For example, the geographic origin of bird migration prompts the debate on whether the ancestors of migratory birds originated in low-latitude nonbreeding areas or high-latitude breeding areas (the so-called southern home and northern home hypotheses) (127) (**Figure 2***c*). The former suggests that migratory birds evolve from tropical, nonmigratory ancestors and develop migration patterns as they shift their breeding grounds from the tropics to the temperate zones. The latter, in contrast, posits that migratory birds develop their migration patterns by shifting their nonbreeding ranges from ancestral high latitudes toward the tropics. Although these hypotheses have gained popularity, reconstructing evolutionary changes in migration patterns over time has proven to be complex and challenging.

Advances in phylogenetics and biogeography provide new insights and opportunities for exploring these issues. Winger et al. (128) tested the northern versus southern home hypotheses using approximately 800 songbird species in the western hemisphere. The results showed that long-distance migration evolved many times in this group as various species shifted their

nonbreeding range to lower latitudes, whereas it was less common for species to evolve migration via shifts of their breeding range out of the tropics (128). The study also revealed that many groups of sedentary, tropical species are descendant from migratory ancestors that had lost migration and stayed in the tropics. The comparisons contradict the southern home hypothesis and suggest that migration evolved most commonly in birds that originally were found in the north (128).

Subsequently, Zink & Gardner (129) raised concerns about the above study (128) for not considering the unequal living conditions at various latitudes when studying the evolution of migration. Additionally, studies using ancestral state reconstruction approaches also face challenges in interpreting trait evolution, as demonstrated by Ponti et al. (130), who used *Sylvia* warblers to study the evolution of migration and assess the impact of different elements such as branch length estimation, trait coding, statistical framework, and taxon sampling. Despite these challenges, with the increasing number (N = 363) of bird genomes being sequenced (131) and the emergence of more comprehensive statistical models, studying the origin and evolution of bird migration from a systematic genomics perspective seems to be very promising in the future.

4.3. Environmental Changes and Ongoing Evolution of Bird Migration

Migratory birds have been shown to be sensitive to climate change, and research has demonstrated that past climate change had already influenced the evolution of bird migration (132). Recent advancements in understanding the response of bird migration to changing climates have been made (**Figure 2***c*), including the suggestion that birds can either switch off their migratory behavior or maintain their migration while shifting their range in response to glaciations (129, 133, 134). Genome-based methods have also provided strong support for reconstructing past demography and deepening our understanding of bird migration (e.g., 43, 47).

However, we are currently in the Anthropocene era, a period marked by rapid climate change, such as the unprecedented rising of global temperature, due mainly to human activities (135). As temperatures continue to rise, many bird species have been found to change their migratory strategies, with some birds advancing their migration time (136, 137), potentially resulting in reduced breeding success rates (138). Additionally, rising temperatures can alter the migration distance of birds, with long-distance migratory birds being at risk of losing breeding and wintering habitats, as well as facing longer migration distances, due to intensified global warming (139).

Moreover, the changes in climate could also cause birds to evolve new migration routes (**Figure 2***c*). One example is Richard's pipit (*Anthus richardi*), a migratory songbird that breeds in the Siberian grasslands and winters in Southeast Asia. Dufour et al. (140) found that the species has become a regular autumn and winter visitor to western Europe only recently, likely because of an increase of wintering niche suitability due to climate change.

Despite some migratory bird species being able to adapt or respond quickly to climate change, it may be insufficient to mitigate the adverse impacts of climate change on their migratory patterns. For instance, Schmaljohann & Both (141) conducted a review of 49 tracking studies and quantified the potential range of adjusting spring arrival dates through modifying migration speeds. They found that among-individual variation in migration speed was determined mainly by the relatively short stopover duration. By assuming that this population response reflects individual phenotypic plasticity, they calculated the potential for phenotypic plasticity to speed up migration by reducing stopover duration. However, the flexibility in the major determinant of migration duration seems insufficient to adjust to ongoing climate change and is unlikely to explain some of the observed arrival advancements in long-distance migrants (141). Similarly, a meta-analysis of 71 bird studies showed that species with adaptive phenotypic responses may be evolving too slowly to keep pace with global climate change (142).

5. CONCLUDING REMARKS AND FUTURE PROSPECTS

The study of the genetics and evolution of bird migration is a constantly evolving field that has witnessed significant advances in recent years. Looking ahead, there are several promising areas for future research in this enigmatic field.

5.1. Molecular Mechanisms of Migration

Although past studies have shown that genetics plays an important role in migratory strategies, we still have much to learn about the specific genes, gene interactions, and molecular pathways involved. To gain a deeper understanding of molecular mechanisms of migration, future research should use omics technologies to study the genetic basis across a wide range of bird species. By comparing genomes of different bird species or populations with varied migratory strategies, researchers can identify target genes and genetic variations associated with migration and investigate their evolutionary origins. This approach has already yielded valuable insights into the genetic basis of migration and is highly likely to continue to contribute to our understanding of bird migration in the future.

5.2. Elaborate Functional Experiments

Previous studies using various methods such as candidate genes, genomics, transcriptomics, and epigenetics have identified numerous genetic variations relevant to migration behavior; most, however, still lack evidence of functional significance. In addition, to our knowledge, there is still no implementation of gene-editing technology in the study of migratory birds. Therefore, more elaborate functional experiments are needed to fully understand the direct effects of these identified genetic loci on bird migration. Meanwhile, it is also important to evaluate and control the potential risks associated with genetically modified organisms once they are released to the wild.

5.3. Evolutionary Origin of Bird Migration

Studying the evolutionary origin of bird migration is an area of active research. The use of phylogenetic and phylogeographic approaches has spurred significant progress in this field, but many important questions remain unexplored (e.g., Where are the evolutionary origins of bird migration?). With more and more bird genomes being sequenced, systematic tests on various hypotheses using phylogenomic-based methods, along with reconstructed long-term paleoclimate or geochemistry data, could facilitate our understanding of the evolution of bird migration.

5.4. Migratory Strategies in Response to Climate Change

The impacts of climate change on migratory birds are a significant concern, as changing climate conditions can disrupt migratory patterns and threaten the survival of these species. To better understand how migratory birds respond to climate change, future research could investigate the evolved strategies of these birds in response to such changes and identify adaptive genes that may hinder or facilitate their future survival. This knowledge will be key to developing target strategies for mitigating the impacts of climate change on migratory birds.

In summary, although the prospect is promising, research on the genetics and evolution of bird migration is still as full of challenges as ever. One such challenge is how to effectively process and analyze large amounts of data, especially when more and more whole-genome and real-time tracking data are produced. The solution is far beyond classical fields such as animal behavior or genetics, but luckily, interdisciplinary collaborations have already begun to form between researchers from different fields, such as mathematics, physics, and biology.

DISCLOSURE STATEMENT

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