



Annual Review of Ecology, Evolution, and Systematics

Animal Migration: An Overview of One of Nature's Great Spectacles

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Annu. Rev. Ecol. Evol. Syst. 2021. 52:479–97

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

<https://doi.org/10.1146/annurev-ecolsys-012021-031035>

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Keywords

behavioral syndrome, evolution, movement ecology, threshold trait, tracking

Abstract

The twenty-first century has witnessed an explosion in research on animal migration, in large part due to a technological revolution in tracking and remote-sensing technologies, along with advances in genomics and integrative biology. We now have access to unprecedented amounts of data on when, where, and how animals migrate across various continents and oceans. Among the important advancements, recent studies have uncovered a surprising level of variation in migratory trajectories at the species and population levels with implications for both speciation and the conservation of migratory populations. At the organismal level, studies linking molecular and physiological mechanisms to traits that support migration have revealed a remarkable amount of seasonal flexibility in many migratory animals. Advancements in the theory for why animals migrate have resulted in promising new directions for empirical studies. We provide an overview of the current state of knowledge and promising future avenues of study.



HISTORICAL PERSPECTIVE

Throughout history, people have been drawn to the phenomenon of animal migration, pondering how and why some animals make their way across mountains and oceans they have never seen before. This curiosity has led to thousands of scientific books and articles as succeeding generations developed better tools for finding answers to these questions.

The field of animal migration has been ably reviewed in older texts (e.g., Newton 2008, Milner-Gulland et al. 2011, Dingle 2014). Dingle covers the fundamental questions about migration. What is it? Who does it? Why do it? How to do it? What determines timing, distance, and direction? And what are migration's ecological and evolutionary consequences, including with respect to human dimensions? A search of the Web of Science on November 23, 2020 for the words "animal" and "migration" revealed 20,544 entries between 1900 and 2020. Reflecting the explosion of scientific knowledge in all areas, the number of entries for the past 20 years was 17,972, and for just the past 10 years, it was 12,319. It is easy to see that reviewing the field of animal migration presents a challenge.

Our goal for this review is to provide readers with a brief summary of major recent achievements in the field of animal migration, a sense of the main areas of debate, and a view of research questions still remaining to be pursued or identified. We chose to include multiple taxa, while acknowledging that our expertise is in bird migration. To compensate, we asked highly recognized scientists in the fields of animal migration who study different taxa for their direction (please see the acknowledgments). Accounting for the taxonomic expertise of the people we surveyed, there was a high degree of overlap between their suggestions and highly cited articles on the Web of Science.

Within the past 10 years, experts have focused on different kinds of migration (e.g., facultative, partial, and altitudinal) (Barçante et al. 2017, Menz et al. 2019, Åkesson et al. 2020), different taxa beyond birds (e.g., marine megafauna, terrestrial mammals, insects, fish, and bats) (Chapman et al. 2015, Hays et al. 2016, Gnanadesikan et al. 2017, Joly et al. 2019), and different abilities of migrants (e.g., timekeeping and navigation) (Merkle et al. 2019, Åkesson & Helm 2020, Hays et al. 2020). Equally active subfields include the evolution of migration, its impact on species interactions, and its conservation (Bowlin et al. 2010, Winger et al. 2012, Davidson et al. 2020, Winger & Pegan 2020).

Migration is a common attribute across the animal kingdom worldwide (reviewed by Milner-Gulland et al. 2011). Insects and mammals migrate in most regions of the globe, and fish migration is common in both salt- and freshwater ecosystems. Birds migrate on all continents and in all oceans, with several terrestrial bird-migration systems accounting for several hundred migratory species each, including Nearctic-Neotropical migration, which involves migration between North American breeding grounds and Neotropical wintering grounds; Palearctic-Paleotropical migration, which involves migration between Europe or Asia and tropical regions of southern Asia and central and southern Africa; and austral migration, which involves migration between south-temperate latitudes of Australia or South America and sites to the north, closer to the equator (Dingle 2008, Jahn et al. 2020).

Other types of migration may not be geographically limited. For example, in altitudinal migration, animals generally breed at higher elevations, then migrate downhill for the nonbreeding season, a widespread pattern in birds (Barçante et al. 2017, Tsai et al. 2021). Additionally, intratropical migrations of birds, which occur wholly within the tropics, are still poorly understood and likely to be more common than currently appreciated (Jahn et al. 2020).

Given the rich history and broad taxonomic and geographic coverage of animal migration research, a brief review can hardly be all inclusive, and this article has a bias toward birds because



they are the most studied group and because we study birds. However, we have been as inclusive as we are able.

OVERVIEW

The newly emerging field of movement ecology has advanced our understanding of the why, where, when, and how of migration by formalizing a definition of the migratory trait (Nathan & Giuggioli 2013). Definitions for migration can be contentious. How does migration differ from dispersal? Does it require a round trip? Is it migration if an individual completes only a part of a journey that requires multiple generations to initiate and complete? A common use of the word refers to directional movement from a known region to an unknown region, often in relation to resource pulses, often in a direction shared with conspecifics, and often involving a return to the starting point. But if an author called a given movement migration, we considered that a sufficient basis for consideration.

At the population level, migration can fall into three broad categories. These categories are observed across most taxa and include obligate, irruptive, and facultative migration. At the individual level, it can be categorized based on the external cues and internal mechanisms that determine whether and when migration occurs. Here, we briefly describe different categories of migration.

Obligate migration occurs when all individuals from a population migrate at roughly the same time each year. It is common in regions where climate and resource availability are suitable during reproduction and offspring development but suboptimal at other times of the year. As such, obligate migration is more common in temperate regions.

Irruptive migration can occur in any season and typically involves movements of entire populations. In birds, irruptive migrants are nomadic and migrate when limited resources become depleted. The cues that initiate irruptive migrations include diminishing resources but frequently also involve a social component, as is evidenced by the sudden movements of entire populations. In mammals, Gnanadesikan et al. (2017) identified three patterns of movement, including one in which movement involves continuous tracking of a mobile source of energy, such as prey or seasonal green-up, and observed that this pattern varied in relation to species' diet, body mass, and mode of locomotion. Aikens et al. (2020) focused on data from 61 populations of four ungulate species and confirmed that migratory behavior was found where spring green-up was short lived and moved in waves across the landscape. These mammalian movement patterns are consistent with irruptive migration.

Unlike in obligate or irruptive migration, facultative migration occurs when individuals from a population migrate after reproduction in response to conditions and/or environmental stressors. As such, individual migratory strategies may change from year to year, depending on the environment. Studies across taxa have found a range of environmental factors that contribute to the occurrence of facultative migration, such as storms, low food availability, icing up, etc. Facultative migration is sometimes classified as a category of partial migration (defined below) if individual strategies are inconsistent from year to year (Chapman et al. 2011). Facultative migration is common in regions where interannual conditions in the breeding range are highly variable.

Partial migration, in which some individuals of a population migrate while others remain resident year-round, can be obligate or facultative depending on whether individual strategies are consistent across years. Partial migration is found across animal taxa and has been reviewed by Chapman et al. (2011). It has been described in mammals (Cagnacci et al. 2011), insects (Menz et al. 2019), birds (Jahn et al. 2010), and fish (Chapman et al. 2012).

Focusing on within-population variation in movement, we can ask why individuals vary in whether they migrate. Broadly, individuals with greater vulnerability to seasonal conditions



REVISITING OLD ASSUMPTIONS WITH NEW TECHNOLOGIES

More than 40 years ago, Ketterson & Nolan (1976) studied the dark-eyed junco (*Junco hyemalis*) in winter, and based on museum skins, citizen-science observations, and data on vital rates from the field, they concluded that females make longer migrations than males, which they referred to as differential migration. Asking why and how differential migration might occur, they based their conclusions on assumptions of equilibrium population dynamics and trade-offs (Ketterson & Nolan 1983). They determined that males experienced greater mortality during winter than females, probably returned earlier to the breeding range than females, and probably benefited more than females from early return. They speculated that the larger body size in males made them better able to fast during winter storms. They also concluded that the sexes have similar annual survival but that the causes of mortality differ. Males are more likely to die during winter, females during migration, but the authors could go no farther given the methodological limitations of the time. Tracking methods and advances in integrative and population biology make now the right time to revisit the accuracy of previous assumptions so that they may be applied more generally.

outside of the breeding season are most likely to migrate, such as individuals that are subdominant to others and thus less likely to gain access to diminished resources (Chapman et al. 2011). Dominance status often differs with size, sex, or age. In fish, birds, and ungulates, females and young individuals are most likely to migrate away from their breeding grounds following reproduction, although there are exceptions (e.g., Jahn et al. 2010). However, another view is that migration would also benefit individuals that do not migrate if the only consideration were overwinter survival, but for those that remain, there are benefits to site fidelity that outweigh the risks of remaining in place. Studies that use within-population variability in migratory phenotypes have led to important hypotheses concerning both evolutionary and organismal mechanisms that underlie the migratory phenotype (Chapman et al. 2011, Pulido 2011, Watts et al. 2018).

An important category of obligate migration, differential migration, occurs when migration distance varies across different segments of a population. A common pattern in differential migration is that longer migrations are taken by females or young birds. Differential migration was examined closely in the dark-eyed junco (*Junco hyemalis*) (see the sidebar titled Revisiting Old Assumptions with New Technologies) in the 1970s and 1980s. Looking back on differential migration by sex, researchers studying other species have also reported longer migrations by females (Evans & Day 2001), but this is not always the case (Briedis et al. 2019). Among northern flickers (*Colaptes auratus*), males travel farther than females (Gow & Wiebe 2014), and among western bluebirds (*Sialia mexicana*), young females are the sex-age class least likely to migrate, which is least consistent with earlier studies (Dale et al. 2019).

THE MIGRATORY PHENOTYPE

In this section, we take an approach to migration that focuses on the organism and integrative biology. The migratory trait, regardless of the type of migrant, involves directed movement with attributes that include distance, direction, and timing and is made up of steps, phases, and life-time tracks. Movement is brought about by phenotypic attributes of organisms that are flexibly expressed. The migratory phenotype is one in which the whole body, the organism, prepares and executes migration, and it is reflected in the organism's behavior, physiology, and morphology (Piersma & van Gils 2011).

Dingle (2006) uses the term migratory syndrome to refer to the coexpression of phenotypic traits that enable migration and distinguish nonmigratory from migratory forms. Specific



phenotypic attributes, or subtraits, that accompany the migratory phenotype include increased appetite and energy storage, changes in a preferred movement direction, reduced fear of the unknown, suppression of reproductive organs, reprogramming of the gastrointestinal tract, and alterations to the nature of muscle fibers (Dingle 2006, Piersma & van Gils 2011, Velten et al. 2016, Menz et al. 2019). Animals may become hyperactive and hyperphagic. They may switch from diurnal to nocturnal activity, alter their diets, and in insects, even grow wings (Zhang et al. 2019). When these attributes cooccur, they have been said to form a syndrome.

Dingle emphasizes that migratory syndromes represent a convergence of traits across diverse taxa to meet the exigencies of migratory movement by insects, fish, birds, and many other migratory organisms. Others question the existence of syndromes (Piersma et al. 2005, Zink 2011). Because preparation and execution require numerous changes to the nonmigratory phenotype, Piersma & van Gils (2011) refer to within-individual seasonal differences in migratory and nonmigratory phenotypes as phenotypic flexibility, a form of reversible phenotypic plasticity.

Estimating the heritability of migratory traits and correlations between traits is also important but challenging. For example, the heritability of migration distance is difficult to quantify for both offspring and parents in the wild and impossible to measure in captivity in most taxa. However, in many nocturnally migrating birds, nighttime activity in captivity has been used as a proxy for migration distance (e.g., Pulido & Berthold 2010). For over half a century, avian studies have used nighttime activity to identify migratory behavior in captive migrants to estimate heritability of the onset, duration, and termination of migration using full-sib correlations, parent-offspring covariance, and selection experiments. While heritability estimates for different measures related to the timing of migration range from less than 0.03 to 1, much less is known about genetic correlations between the various components of migration (Newton 2008).

THE MIGRATORY PROGRAM

Another approach to the migratory phenotype is the migratory program, which is best understood in birds. According to Åkesson & Helm (2020, p. 1), “The majority of songbirds rely on a genetic program inherited from their parents that will guide them during their first solo-migration.” The phenotypic components of the program include time, direction, and distance, and together, they are built on an endogenous circannual rhythm and “are crucial to individual fitness and survival.” In their view, the program is a given, and to explain considerable within-population variation in routes taken and in timing, one has to account not only for genetic variation but also for individual interactions with environmental and social factors, along with learning. In a recent review of a classic translocation study undertaken by A.C. Perdeck (1958), Piersma et al. (2020) highlight the challenges in interpreting the relative influences of genes, ontogeny, and social and environmental factors on individual migratory decisions. Over four decades, Perdeck and colleagues translocated 18,000 European starlings (*Sturnus vulgaris*) of different ages and migration histories across western Europe and used recovery locations following migration, after displacement, to assess the influence of learning on migration direction. These classic studies and more recent ones (Thorup et al. 2007) have been cited dozens of times as evidence for an innate migration direction in birds. However, Piersma et al. (2020) argue that many noninnate factors were not accounted for in Perdeck’s original studies (e.g., the influence of the social makeup of the migrating flocks or the learning that might have occurred prior to translocation), highlighting the challenges of uncovering the factors that underlie decisions made by migrating animals.

Another major obstacle has been characterizing the genetic architecture underlying migration, the details of which we are only now beginning to understand in birds (e.g., Toews et al. 2019, Bingman & Ewry 2020) and other taxa [e.g., fish (Harrington et al. 2021), insects (Merlin



et al. 2020)]. Significant progress has been made in elucidating the genetics underlying specific tasks necessary for successful migration, such as navigation (e.g., Bingman & Ewry 2020), timing (Ralston et al. 2019), fat and glucose uptake, metabolism, and oxygen delivery (Fudickar et al. 2016b, Franchini et al. 2017, Sharma et al. 2018, Horton et al. 2019). Studies using a candidate gene approach have reported associations between polymorphisms in the genes *Clock* and *Adcyap1* and the timing, duration, and distance of migration in birds (Peterson et al. 2013; Bazzi et al. 2015, 2016; Ralston et al. 2019; but see Contina et al. 2018). Further, there is some evidence of interactions between variants of these genes and correlations with the timing of migration during spring and fall (Ralston et al. 2019). Future research that investigates epigenetic mechanisms of migration is needed to provide critical insight into the complexity of the migratory phenotype. For example, a recent study found that in migratory barn swallows (*Hirundo rustica*), migration phenology was associated with increased CpG methylation of *Clock* (Saino et al. 2017).

In monarch butterflies (*Danaus plexippus*), Zhan et al. (2014) found regions across the genome that strongly differentiated between migratory and nonmigratory forms, along with candidate genes involved in flight muscle development. With respect to timing, Iiams et al. (2019) identified genes and pathways in monarchs related to the detection of photoperiodic cues necessary for inducing migratory behavior. The development of molecular tools, such as knockouts of circadian clock genes to determine their role in migratory behavior in monarchs (Zhang et al. 2017), provides substantial insight into the molecular basis of migration. Despite progress in elucidating the role of specific gene regions, little evidence has been found in support of a common genetic basis for migration across taxa (Delmore et al. 2020). Although there are still more questions than answers, the era of genomics research promises a more detailed understanding of the underpinnings of migration (e.g., Delmore et al. 2016, Lundberg et al. 2017, Merlin et al. 2020, Waples et al. 2020).

THE MIGRATORY THRESHOLD

Traits, syndromes, and programs can be encompassed by the concept of a migratory threshold (Pulido et al. 1996). The migratory threshold model posits that the inheritance of migratory behavior is based on a polygenic threshold model and that migration is a dichotomous trait (migrant or resident) in which an individual's migratory phenotype results from the inheritance of enough migration-associated genes to exceed a threshold. More recently, Pulido (2011) built on the original threshold model to incorporate facultative migration as an intermediate phenotype between obligate migration and obligate residency. In the environmental threshold model of migration, Pulido (2011) describes the relationship between migration propensity, amount of migratory activity expressed, and sensitivity of such expression within a population to environmental variation. By allowing for individual and population variability in internal (i.e., genetic) and external influences, the environmental threshold model begins to account for the myriad of variables that underlie what has been historically treated as a dichotomous trait.

Recognizing syndromes, programs, or thresholds, whose exact characteristics vary among taxa, leads to questions about the evolution of complex traits and whether subtraits are inherited as a complex or segregate independently. As with any integrated phenotype that consists of united expression of subtraits, migration may be the adaptive result of correlational natural selection (McGlothlin & Ketterson 2008). And, if so, a mismatch between normally correlated traits is likely to be maladaptive. To state the obvious, if the direction in which an individual travels is not matched to the distance it travels, the combination could be fatal in the case of a prolonged seaward migration by a terrestrial organism. When considering individual responses to current and future environmental change, the rate of response to selection in a migratory syndrome is likely to



depend in part on the organism's ability to induce or suppress the migratory syndrome as a whole or independently express components of its syndrome. There is mixed support from emerging data on the genetic basis of migration as to whether migration is inherited as a complex phenotype. Some conclude that migration is a polygenic trait composed of many alleles of small effect (Pulido & Berthold 2010). However, a recent study reported that ecotypes in migratory salmon associated with early and late timing of return to streams are the result of variation at a single locus (Thompson et al. 2020). Zera & Brisson (2012) offer a useful summary, as do Saastamoinen et al. (2018), of the genetics of dispersal and migration.

COSTS AND BENEFITS OF MIGRATION

In this section, we discuss what is new in documenting the costs and benefits of migration. Most studies that we report on relate to birds.

Setting aside history and potential genetic constraints, optimality is the most widely used approach to explain variation among individuals, populations, and species. The optimality approach asserts that, other things being equal, migration evolves or is expressed when the benefits outweigh the costs. Obvious benefits of migration include occupancy of regions during seasons when resources are abundant and avoidance of such regions when resources are in short supply. In particular, food limitation may play an important role in the evolution of bird migration, since migrants are released from competition with residents for food resources (Cox 1968). Migration may also allow for higher winter survival (Winger & Pegan 2020), escape from predators, tracking of prey, and a reduction in interspecific competition (Furey et al. 2018, Teitelbaum & Mueller 2019). Obvious costs include the risks encountered in transit or at the destination, such as novel predators, along with the need to establish oneself in a new location despite a lack of familiarity with local food sources and predators.

To determine the cost of migration, and also whether it is less than the benefits, researchers have traditionally compared annual mortality in sympatric species that do and do not migrate or in allopatric populations of the same species that do and do not migrate. A recent study of 53 passerine species compared population growth rates in migrant and resident species belonging to the same temperate-zone community and found growth rates to be higher in resident species than in long- or short-distance migratory species (Bellier et al. 2018). This contrasts with an older belief that annual survival is greater in Nearctic-Neotropical migrants compared to nonmigratory temperate-zone species, in which greater annual mortality is accompanied by greater productivity, given more time to be reproductive (Greenberg 1980).

More recently, migration has been shown to be the season of highest mortality in migratory birds. Examples include the Kirtland's warbler (*Setophaga kirtlandii*), for which the cost of migration was deduced by calculating breeding season and winter season survival in relation to annual survival and determining migration mortality through subtraction. Mortality was much higher during migration than other seasons (Rockwell et al. 2017). A similar approach applied to the wood thrush (*Hylocichla mustelina*), in which apparent mortality was obtained by subtraction from known rates of winter and summer survival, again showed mortality to be greatest during migration. Further, mortality was greater during spring migration than in fall (Rushing et al. 2017).

Given the inherent risks in traveling through unknown landscapes, including newer risks such as dams, fences, window strikes, and domestic cats (*Felis catus*), researchers have focused on determining vital rates of migratory populations and the fates of individuals that migrate. A huge push has also been made to develop tools that allow individuals to be followed through their full annual cycle (Kays et al. 2015). By tracking individuals with tags or via citizen monitoring groups, we can ask, Which is riskier: a single long-distance migration or one broken into steps? flying over water



or land? in spring or in fall? We can also ask about the effects of location and departure time on arrival time.

Newer studies on the costs and benefits of migration also include a focus on parasites. Migration is recognized as a means for escaping regions with high levels of parasitism (known as migratory escape) despite exposure to novel parasites along the way or at the destination (Altizer et al. 2011). A recent model based on the work of Altizer et al. (2011) considers the impact not just of prevalence but also infection intensity (parasitemia) on migration (Balstad et al. 2020). One study showed that within-population variation in intensity can result in partial migration, in which heavily infected individuals are less likely to migrate.

Another new approach to studying the costs and benefits of migration posits that migration is a means for maintaining the advantages of site fidelity in seasonal environments. Winger et al. (2019) argue that breeding-site fidelity is highly beneficial, and migration should be viewed as one of several adaptations that allow individuals to stay in the same place when highly seasonal environments force them to retreat. Migration should therefore be studied alongside other adaptations to seasonal environments, such as hibernation or freeze tolerance. Migrations of common swifts (*Apus apus*) confirm the advantages of returning to familiar sites (Åkesson et al. 2020). Black-browed albatrosses (*Thalassarche melanophrys*) that forage in the same locations over time have higher reproductive success than those that move around to forage (Patrick & Weimerskirch 2017).

Tracking individuals is the most direct way to measure mortality. Mortality in tagged juvenile white storks (*Ciconia ciconia*) is lower in those making shorter migrations than longer ones (Cheng et al. 2019). Based on sightings of color-marked Eurasian spoonbills (*Platalea leucorodia*), individuals of this species making shorter migrations also had lower mortality (Lok et al. 2015). However, one of the challenges of tracking studies is that sample sizes are still relatively small owing to cost and the battery life of the tags. When an animal's tag ceases to report its location, has the tag failed or has the animal died? Researchers use various tactics to assess tag failure and correct for it when reporting mortality, and fortunately, tag quality is increasing rapidly (Kays et al. 2015). In the near future, results based on tracked individuals are expected to increase exponentially.

EVOLUTIONARY HISTORY OF MIGRATION

Migration is likely an ancient behavior in most if not all avian lineages (Zink 2011), with its expression changing rapidly over time (e.g., Piersma et al. 2005), depending on environmental conditions (Zink & Gardner 2017). Because of these reasons, and because migration is made up of a suite of traits or a syndrome (Dingle 2006), evaluating the evolution of migration depends on the trait. A case in point is wing pointedness in birds, which is key both for migration and for local dispersal in both migrants and nonmigrants (Sheard et al. 2020). Research comparing the development and maintenance of such characters in long- versus short-distance migrants and nonmigrants is key to elucidating the history of the gain or loss of migration, which has occurred multiple times in some lineages such as parulid wood warblers (Winger et al. 2012), new world flycatchers (Chesser 2000, Gómez-Bahamón et al. 2020), and *Catharus* thrushes (Voelker et al. 2013). A further complication is that the capacity to migrate may exist but not be expressed in some lineages (Zink 2011). For example, similar to migrant stonechats, nonmigratory equatorial stonechats (*Saxicola torquata axillaris*) express nocturnal activity when held in captivity, despite an estimated 1 to 3 million years since their divergence from a common migrant ancestor (Helm & Gwinner 2006). Helm & Gwinner (2006) proposed that readiness to migrate could be common in most birds and that an endogenous circannual migration program can be activated when favored. Ultimately, understanding where and how migration evolves and is regulated rests on our ability to tease apart



the genetic versus environmental control of migration at a broad taxonomic scale while considering the consequences of the migratory phenotype on fitness (Liedvogel et al. 2011, Merlin & Liedvogel 2019).

Numerous attempts have been made to postulate a geographic origin for migration in different bird migration systems, such as a southern home origin (Levey & Stiles 1992), a northern home origin (Winger et al. 2014), a subtropical origin for Nearctic-Neotropical migrants (Cox 1985), or the shifting home hypothesis in the Palearctic-Paleotropical system (Louchart 2008). Such attempts are likely to lack generality across taxa. What is increasingly apparent across multiple avian lineages is that migration is generally driven by both a need to track spatially and temporally varying food resources (Somveille et al. 2015) and a need to avoid harsh climatic conditions (Boyle et al. 2010). Food, in particular, is likely to play a central role in the initial development of migratory behavior (Boyle & Conway 2007).

MIGRATION AS A MAGIC TRAIT: HETEROPATRY, ALLOCHRONY, AND POPULATION DIVERGENCE

Is migration a magic trait? The term magic trait is used in speciation research to refer to situations in which reproductive isolation arises as a by-product of adaptive divergence (Servedio et al. 2011). If migration gives rise to linked-trait complexes such as a migratory syndrome, and if migration leads to differences in timing of reproduction, then migration can lead to population divergence and can be viewed as a magic trait. Two related concepts that describe how migration may lead to population divergence are migratory divides (Price 2008) and heteropatry (Winker 2010).

Migratory divides describe how migratory behavior can lead to sympatric speciation (Price 2008, Turbek et al. 2018). Divides refer to situations in which closely related populations have overlapping breeding ranges but separate wintering ranges along with separate migratory routes. Divides exist in various taxa, including birds and fish such as sockeye salmon (*Oncorhynchus nerka*) (Wood et al. 2008) and Atlantic eels (*Anguilla rostrata*) (Albert et al. 2006). Differences in non-breeding locations can lead to asynchronous return times to the breeding site that can result in assortative mating based on migratory timing. A now-classic example of a migratory divide and divergence is the blackcap (*Sylvia atricapilla*), an old-world warbler. After a colonizing population began to winter in England and return to Germany to breed earlier than blackcaps wintering further south, assortative mating by migratory strategy followed with clear potential for further divergence (Rolshausen et al. 2009).

Migratory divides can also lead to population divergence when hybrids take migratory routes that are intermediate to parental populations and also disadvantageous. Delmore et al. (2020) tracked 100 individual blackcaps and found that those to the west and east of a migratory divide migrated southwest and southeast, respectively, but those living in the region of the migratory divide took intermediate (south) and riskier routes over the Mediterranean Sea.

In relating migration to population divergence, Winker (2010) noted that many closely related avian populations live together in sympatry for part of the year, but because of movement they become allopatric when breeding; this is the reverse of migratory divides, i.e., separate when breeding but not when wintering. He named this distribution heteropatry and proposed that if hybrids formed between migrants and residents while they were in sympatry but performed more poorly because of a mismatch in their seasonal timing to the local environment, then selection might act against such hybrids. For example, a migrant-resident hybrid that migrated might breed too early for the climate where it settled based on its resident heritage. Conversely a migrant-resident hybrid that did not migrate might breed later than its conspecifics based on its migrant heritage and suffer a fitness disadvantage (Price et al. 1988).



Winker (2010) also predicted that population divergence arising in this way was likely to begin with altered gene expression as opposed to mutation, as recently reported by Saino et al. (2017), followed by genetic accommodation. Winker is not alone in relating differences in seasonal timing to population divergence. Students of sympatric speciation have long written about the potential for timing differences (allochryony) to create circumstances favorable to divergence. For example, Gómez-Bahamón et al. (2020) found that breeding allochryony between resident and migratory subspecies of fork-tailed flycatchers (*Tyrannus savana*) in South America is a product of a loss of migration by the residents. A phylogenetic analysis conducted at the family level suggested that switches in migratory behavior may represent an important yet poorly understood mechanism of diversification in flycatchers and other birds. de Zoeten & Pulido (2020) also found that a completely migratory population can transition toward complete residency via partial migration when the fitness of residents is high enough. If, as they predicted, resident populations retain substantial cryptic genetic variation related to an ability to migrate, subsequent reversals could occur rapidly.

Recent research has compared migratory and reproductive timing in closely related, seasonally sympatric populations of the dark-eyed junco (*Junco hyemalis*) that winter together but breed in allopatry. Fudickar et al. (2016a) found fixed differences in timing between resident and migratory populations in the sense that the differences persisted in a common environment. Such fixed timing differences may preclude hybridization, but other seasonally sympatric populations of juncos were shown to be more flexible in timing (Fudickar et al. 2017). A recent study of resident and short-distance migratory juncos demonstrated that residents exhibit a lower photoperiodic threshold and initiate reproductive development earlier in the year, whereas reproductive development is delayed in migrants (Singh et al. 2021). Interestingly, exposure to light at night accelerated reproductive development in both migrants and residents (Singh et al. 2020). An extreme example of how migration can lead to range expansion is the barn swallow (*Hirundo rustica*), which has recently established a breeding population in Argentina (Winkler et al. 2017). This species has migrated between North American breeding grounds and wintering grounds in Argentina and continues to do so. Yet in the 1980s, some swallows were found to be nesting in bridges in Argentina. The Argentinian breeding population is now an austral migrant, spending its nonbreeding season in northern South America (Winkler et al. 2017). Population divergence seems likely to follow.

EMERGING TECHNOLOGIES AND EMERGING PATTERNS

Huge strides are being made in studying patterns and processes. Our ability to observe and quantify migration has been staggeringly enhanced by technology allowing the use of tags deployed on individual migrants to follow their paths throughout the year and determine their rate of movement, direction, and pathways between breeding and nonbreeding locations. A sample of published studies and data are available to all in the Movebank Data Repository (<https://www.movebank.org/cms/movebank-content/data-repository>). As of January 5, 2021, Movebank was populated by 3 billion locations, including 5,882 studies on 1,020 taxa.

The innovations allowing for these observations center around the miniaturization of tags for animals as small as insects (Knight et al. 2019). In addition, knowledge of the timing of migratory movements by birds and butterflies, for example, has been enabled at new scales by contributions of community scientists to databases such as eBird (<https://ebird.org>) and eButterfly (<https://www.e-butterfly.org>). Population declines of migratory birds have also been

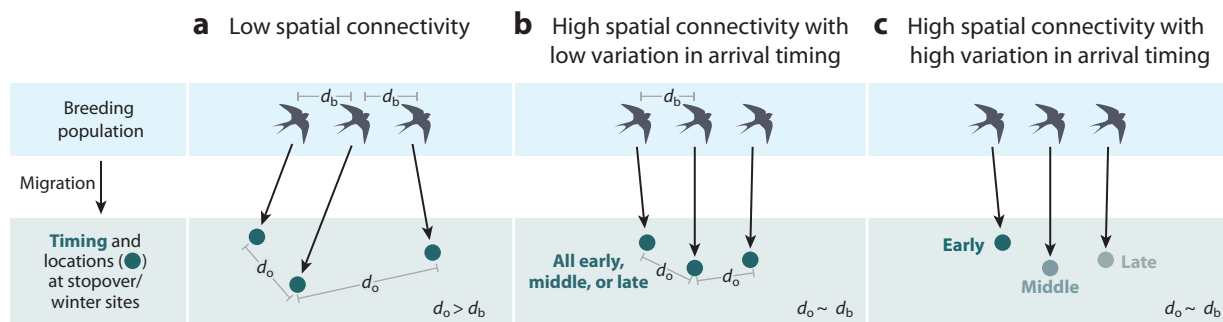


Figure 1

Conceptual model of migratory connectivity and timing of arrival at stopover/winter sites between individuals of a breeding population. Each panel represents the connectivity of individuals from a single breeding population. (a) Spatial connectivity is low when the distance between individuals is higher outside of the breeding season (d_o , bottom row) versus during breeding (d_b , top row). Conversely, spatial connectivity is high when the distance between individuals outside of the breeding season is similar or lower as compared to during breeding. In the latter case, there can be (b) low or (c) high variation in the dates individuals arrive at a stopover/winter site. For a discussion of spatial and temporal migratory connectivity across populations, see Knight et al. (2021). Figure inspired by Knight et al. (2021).

documented by community scientists on the ground and by radar tracking of the sky (Rosenberg et al. 2019).

Bio-logging, or the use of electronic devices attached to organisms, has been undergoing a revolution in its miniaturization and precision, allowing researchers to study movements of large and small organisms alike and resulting in unprecedented discoveries (Kays et al. 2015). For example, data from light-level geolocators have shown that blackpoll warblers migrate over the ocean, non-stop, for up to three days (DeLuca et al. 2019) and that a 25-g bird, the northern wheatear (*Oenanthe oenanthe*), migrates up to 29,000 km annually during a round trip between Alaska and Africa (Bairlein et al. 2012). The use of satellite transmitters has revealed details of flights of bar-tailed godwits (*Limosa lapponica*) over the Pacific Ocean (Gill et al. 2005) and long-distance migrations of flying foxes (*Pteropus poliocephalus*) (Roberts et al. 2012), loggerhead sea turtles (*Caretta caretta*) (Mansfield et al. 2017), white sharks (*Carcharodon carcharias*) (Bonfil et al. 2005), and humpback whales (*Megaptera novaeangliae*) (Riekkola et al. 2020).

Another technology permitting detailed research on timing of migration is weather radar, which has been increasingly useful as methods for extracting relevant data have advanced (Schmaljohann 2020). Notably, by combining different tracking methods, additional aspects of an animal's biology during different phases of migration can be studied, such as the temperatures it experiences (Dunn et al. 2020) and the number of days it spends flying versus resting [e.g., using accelerometers (Hedenström et al. 2016)]. Further, intrinsic markers such as genes and stable isotopes have proved useful in studying migratory movements in various taxa and supplementing information collected from tagged individuals (Ruegg et al. 2014, Hobson et al. 2020). Additionally, novel modeling techniques and software packages are allowing increasingly refined analyses of movement data (e.g., Noonan et al. 2019).

The rapidly increasing number of data sets has resulted in novel methods for describing and monitoring connections within and between populations throughout the seasonal movements of migratory animals. Migratory connectivity is a measure of the spatiotemporal overlap between individuals of the same or different populations as a result of migration (Bauer et al. 2016, Cohen et al. 2019, Knight et al. 2021) (Figure 1) and is critical for evaluating the events that define the annual cycle of migratory organisms (Marra et al. 2015), including population dynamics (Hostetler

et al. 2015) and the relative risk of a population and/or species due to environmental change (Finch et al. 2017). Emerging technologies are increasingly enhancing our ability to describe migratory connectivity in more detail and across more taxa.

FUTURE DIRECTIONS

When we step back and look at the big picture, it is apparent that the field of animal movement research is experiencing a revolution, in large part due to emerging techniques and technologies that continue to provide novel and surprising insights. We are now able to study processes at ever-finer spatiotemporal scales. Future research across molecular, organismal, population, and community levels is necessary to unveil the selective pressures driving the evolution and regulation of migration, the factors that mediate it, and its consequences.

Examples of questions that promise to significantly advance our understanding of the cognitive and physiological mechanisms mediating migratory behavior include (a) What is the genetic basis of migration in different taxa, and what components of the environment determine whether (and how strongly) the genetic component is expressed? (b) To what extent are the genetic components of migration conserved over different durations of ancestral nonmigratory periods? (c) What is the relative contribution of extrinsic (e.g., photoperiod) versus intrinsic (circannual) mechanisms that determine whether and when to move? (d) How do these relationships change throughout the year and across an individual's lifetime to affect its fitness? One way of addressing some of these questions is by combining experimental and observational approaches, for example, by studying movement patterns using tracking devices after manipulating an individual's physiology or exposure to cues, and doing so across closely related taxa that move in different contexts, to understand the generality of the results.

Additionally, given the advent of technologies available to track the movements of individuals at small spatiotemporal scales, evaluating results of studies conducted prior to the current technological revolution could offer new insights. For example, to evaluate the drivers of differential migration by dark-eyed juncos (*J. hyemalis*), Ketterson & Nolan (1976) used techniques that required several assumptions to infer patterns, since the fates of individual birds were unknown (see the sidebar titled Revisiting Old Assumptions with New Technologies). Looking back, several of these assumptions are held across most migratory types (e.g., obligate, facultative), so we think that a brief discussion is relevant for the general reader. The following assumptions made in that study could be revisited:

1. Greater abundance of females wintering farther from the breeding range than males is evidence for longer migrations. Studies in the meantime have confirmed that females migrate farther, although with exceptions (Gow & Wiebe 2014). Distance can now be measured directly by tagging males and females on their breeding range and tracking their migratory paths and destinations to determine distance migrated.
2. The farther individuals migrate, the later they return to the breeding range, because arrival time is dictated by migration distance. A recent study showed that white storks (*C. ciconia*) wintering closer to the breeding range arrived earlier, but those that traveled farther arrived in better condition owing to more favorable overwinter sites, exhibiting a carryover effect (Rotics et al. 2018). Another recent study using migration tracking data from 26 bird species found that migration distance predicted spring arrival date, with 1,000 km corresponding to a 2-day delay in arrival (Schmaljohann 2019). Dates of arrival and speed of migration can now be measured directly by tracking tagged animals.



3. Early-arriving males have higher reproductive fitness, but arrival time does not covary with fitness in females. Kokko et al. (2006) modeled arrival time in birds and concluded that early-arriving individuals have greater reproductive success and that males benefit more than females, particularly when extrapair fertilizations are included in the analysis and role-reversed species are excluded. Morrison et al. (2019) report that early arrival results in higher fitness in part because it leaves more time for replacement clutches in the face of nest predation. Arrival time can now be measured with precision and needs to be measured in the field in relation to reproductive success in males and females.
4. The farther individuals migrate, the greater the cost because migration mortality is distance dependent. Migration mortality is greater in females than males because they make longer migrations. A recent study of juvenile white storks (*C. ciconia*) showed that en route mortality is lower in those making shorter migrations (Cheng et al. 2019). Still, estimations of the cost of migration need to consider carryover effects (Briedis et al. 2018). Of course, there are exceptions. Common cuckoos (*Cuculus canorus*) that breed in Great Britain and cross the Sahara to overwinter exhibited greater mortality if they took the shorter route southwest through Spain compared to a longer eastern route through Italy and the Balkans (Hewson et al. 2016). Now that tracking individuals year-round is possible, these assumptions can be measured directly with tags.
5. Individuals making shorter migrations to overwinter in harsher environments suffer higher winter mortality but lower migration mortality and thus have similar annual survival. Now that tracking individuals throughout the full annual cycle is possible, these assumptions can be measured directly with tags.

Some of the assumptions made in the mid-1970s have been confirmed through observation and comparative studies or by modeling. With respect to carryover effects, which were not initially considered, we have learned that wintering in more distant but milder climates may allow migrants to return in better condition. Further, any similar study conducted today would do well to consider the role of pathogens.

To reveal how individual-level processes, such as migration timing and distance, translate to fitness, and ultimately to population outcomes such as growth or decline, an integrative approach that considers carryover effects throughout the annual cycle is required. Doing so across populations that experience different selective pressures is key to determining whether results in one system are applicable to others, especially in terms of informing conservation and management. Further work on the relationship between migration and population divergence is also needed, since migration has the potential to play an important role in divergence and maintaining genetic diversity across a wide range of taxa (Rolland et al. 2014).

The consequences of migration for the greater ecosystem of which migrants are a part is another compelling area of research, especially given the rapid changes that ecosystems used by migrants are experiencing across the planet. What are the consequences of different types of migratory strategies (e.g., short- versus long-distance migration) on disease and seed dispersal? How does the strength of migratory connectivity impact a migratory host's ability to transmit and disperse pathogens? And how can we expect these processes to look in the future as a consequence of rapid environmental changes, such as urbanization and climate change? An increasingly integrative approach is necessary to answer such questions (Bowlin et al. 2010).

Future work is needed to synthesize the patterns that are emerging and test long-standing hypotheses that were not previously testable. Synthesis and experimentation are the obvious next steps in the field of animal migration, and if employed with an interdisciplinary approach, these



approaches promise many more exciting discoveries on the grand spectacle of migration that has fascinated people throughout history.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The authors heartily thank the following people for their advice on content for this article: Emily Cohen, Hugh Dingle, Micah Freedman, Ran Nathan, Kristen Ruegg, Tony Zera, and Bob Zink. We would like to thank the Environmental Resilience Institute, funded by Indiana University's Prepared for Environmental Change Grand Challenge initiative. A.M.F. and E.D.K. were also supported by the National Science Foundation (award number 1856423).

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