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The Renaissance of Migratory Bird Biology

A Synthesis

NEW APPROACHES TO OLD QUESTIONS

The study of bird migration has fascinated scientists since the early days of ornithological research. Our aim in assembling this book was to provide readers with a sense of renewal in all aspects of the study of bird migration from evolution and ecology to physiology and morphology. The major questions that drive research on migration systems continue to dangle out there like brass rings eluding our grasp: How did long-distance migration originate? How do different events and seasons shape the life history and adaptations of migratory species? How do migratory species interact with resident species? Although we await final answers to these and other questions that may never come, new approaches have been brought to bear on these time-honored issues. As witnessed within this volume, researchers are increasingly integrating studies of migratory birds with other seemingly unrelated disciplines of biology such as biogeochemistry and remote sensing.

The Evolution of Long-Distance Migration

Probably the single most significant improvement in our understanding of the evolution of migration has been the use of molecular genetics to determine the phylogenetic relationships between migratory and resident taxa. Several studies have been published to date (see Joseph, Chap. 2 [All such references herein are to chapters in this volume.]) and it is clear that birds have shown surprising evolutionary lability in

migratory behavior. Although migration has deep roots in the major taxa involved, migratory patterns appear to be quite responsive to environmental change. The development of direct (e.g., fossil evidence) and indirect (e.g., isotopes analyses of climate change) approaches to establish what the paleoecosystems might have been in the regions where migration might have evolved provides a powerful backdrop for understanding these evolutionary studies (Steadman, Chap. 1). The use of new phylogenetic techniques, combined with traditional approaches within historical biogeography, provides a fresh breath for testing specific hypotheses about when and where migration evolved (Outlaw et al. 2003). These same techniques also provide better resolution than morphological analysis for how migratory and nonmigratory taxa are related (Joseph, Chap. 2).

The Diversity of Migration Systems

The diversity of avian migration systems is just becoming apparent. There are six major migration systems around the world: Palearctic-Afrotropical, Nearctic-Neotropical, Palearctic-Asian, Austral-African, Austral-Neotropical, and Austral-Asian (Hayes 1995). Only recently has the extent of migrations from Southern Temperate regions into the tropics (austral migration) been appreciated. Probably because of the limited landmass at high latitudes and the less continental climate of these regions, the diversity of austral migrants has been thought to be low. Also, the state of biogeography of Southern Hemisphere avifaunas still lags behind their boreal equivalents. However, upon close examination, we now know that some of these austral systems are quite diverse. For example, over 220 species of birds from the Southern Cone of South America are now classified as complete or partial migrants (Chesser, Chap. 14). Furthermore, we now have a much better understanding of some of the basic ecological and biogeographical features of at least the South American austral migration systems (Chesser, Chap. 14). We can begin to perceive finer patterns within austral migration systems, similar to those made for Northern Temperate Zone birds. Joseph (Chap. 2) makes a compelling argument that what we have considered to be the austral migration systems involves two very distinct strategies with respect to response to climate. Furthermore, the diversity of movements within tropical regions is receiving increased recognition. Such tropical movements include north/south movements confined to tropical areas—some of which involve crossing the equator to take advantage of different seasonal regimes. Intratropical movements can also involve altitudinal movements of birds (Loiselle and Blake 1992), particularly omnivorous species, and migrations between wet and dry habitats. Given that migration may have originally developed in multiple lineages under more tropical conditions during the early Tertiary (Steadman, Chap. 1), the study of present-day tropical migration systems may provide insight into the ecological prerequisites of migration (Chesser and Levey 1998).

Among landbirds, Old and New World migration systems are dominated by distantly related taxa. Hemispheric comparisons of migratory traits can be quite robust because a shared phylogenetic history is minimal. Such comparisons of unrelated taxa allow for the determination of which features are general and which are responsive to present-day ecological and historical differences between temperate and tropical ecosystems. For example, current conditions in northern Africa are considerably more arid than those in the northern Neotropics, although both regions showed periods of distinct aridity through the Pleistocene. We also know that the vegetation of Europe was more extremely affected during the glaciations than that of North America. The geography of barriers to migration differs as well. How these large-scale and the myriad more subtle differences shaped migration in the two hemispheres is just beginning to be explored in a comprehensive way.

Comparisons between Old and New World patterns is a pervasive theme in many of the chapters in the book. Patterns of distribution of migratory birds across the Holarctic are compared by Mönkkönen and Forsman (Chap. 11). The difference in habitat distribution of migrants in the Western Palearctic and Nearctic is strongly related to differences in habitats in Africa and the Neotropics (Böhning-Gaese, Chap. 11). However, differences in the response of vegetation to Pleistocene events need to be factored into future comparisons between the Old and New Worlds. Greenberg and Salewski (Chap. 26) find similarities in the degree of sociality in migrants in the two hemispheres, with telling differences (such as the lack of highly social and omnivorous Old World tropical migrants). Some of the differences between the New and Old Worlds are unexpected and demand further research to develop explanatory hypotheses. An example of this is the lower frequency of extra-pair fertilization in Old World migratory passerines (Stutchbury et al., Chap. 24). It should be noted that most comparisons focus on Western Palearctic / African migration versus North America (often just eastern North America). In many ways, the Eastern Palearctic is more similar to North America in its present-day habitat and Pleistocene vegetation history. We hope the next synthesis will involve more comparative work with this region as well.

The Nonbreeding Season

Thirty years ago, the Tropics formed a mysterious realm into which migratory birds disappeared for long periods. Perhaps nothing has changed more dramatically than the accessibility of the Tropics and the increase in our knowledge of the natural history of tropical avifaunas, both migratory and nonmigratory. Basic information on the natural history of migratory species on their tropical wintering grounds has increased but this period of the annual cycle is still seriously understudied (Rohwer, Chap. 8; Stutchbury et al., Chap. 24; Froehlich et al., Chap. 25; Greenberg and Salewski, Chap. 26; Runge and Marra, Chap. 28). For some

tropical regions around the world, we have information on the geographic distributions of winter populations of migratory birds and some rudimentary habitat use data for many species, along with anecdotal observations of social and foraging behavior. We are just now beginning to see signs of greater attention to individual species and specific demographic classes within species during the nonbreeding season. However, quantified data have been garnered for only a few well-studied species. Information on the ecology of migrants wintering in East Asia, in particular, is still almost nonexistent.

The Macro-Distribution of Migratory Birds

MacArthur's (1959) focus on breeding landbirds of North America was the first attempt to find patterns in the relative abundance and diversity of migratory and resident birds. As more information has become available, researchers have looked across the different continents to establish general rules governing the distribution of migrant and resident taxa (Newton and Dale 1996). These approaches have generally been applied in accounting for patterns of distribution during the breeding season in the North Temperate Zone, but several authors in this volume have synthesized what we know about the relative importance of climate, habitat structure, and food resources across most of the major migration systems and periods of the annual cycle. Other chapters in this volume introduce innovative approaches to the question of the relationship between the distribution of long-distance migrant and resident birds in both the Temperate Zone and the Tropics. Various studies (Hockey, Chap. 5; Mönkkönen and Forsman, Chap. 11; Böhning-Gaese, Chap. 12; Gauthreaux et al., Chap. 15) each integrate, in their own way, the broad distributional patterns with the ecological processes that might mediate the relationships between migrants and their environment. This new integrated approach to the distribution of migrants is based on an array of concepts, some old and some new: evolutionary origins, global patterns of climate (temperature and wind patterns in the Temperate Zones, rainfall in the Tropics), the properties of ecosystems that contribute to climatic buffering, the seasonality of particular resource types, and the competitive and cooperative interactions between migrant and resident species (and how these change between climatic regimes). These concepts go a long way toward explaining the relative abundance and diversity of migratory and resident species, particularly in the Temperate Zone.

Studies of ecological interactions between migrants and residents in tropical areas have become less popular in recent years. It is increasingly clear from such analyses that our ability to investigate large-scale questions seeking to explain the distribution and abundance of species depends upon a more complete knowledge than we now have of the population ecology of individual species and specific guilds of species.

The Micro-Distribution of Migratory Birds

Avian ecology has traditionally focused on the role of resources (particularly food) in determining the distribution and abundance of species. Evaluating the relationship between migratory bird populations and their food supplies requires sound information on the abundance and seasonality of food and its variation between years and habitats. Furthermore, the data are more interpretable if data on diet are used to help select a resource-sampling scheme that focuses on the relevant prey items. With new attention to empirical evidence, Sherry et al. (Chap. 31) have established a *prima facie* case that food supply is often the most important limiting factor in the distribution and abundance of nonbreeding migratory birds in the Tropics. On the breeding ends of things, annual fluctuations in food supply also underlie variation in reproductive success and this variation appears to have important consequences for population size in subsequent years (Sillett et al. 2000).

Our understanding of population dynamics also requires detailed knowledge of the effect of different predators and parasites (avian brood parasites, ectoparasites, disease-causing microbial agents). The role of nest predators and brood parasites has long been incorporated into breeding season studies of migratory birds. However the effect of predation and disease on adult birds has been more elusive. Recent studies of incidence of human disease (e.g., West Nile virus) in migratory birds underscore their potential as long-distance vectors (Ricklefs et al., Chap. 17) and the topic is certain to receive much more research attention.

The analysis of morphological and behavioral adaptation has become increasingly sophisticated, allowing us to use the traditional comparative approaches with increasing rigor. The multivariate models necessary to handle complex and interrelated traits are far more robust than they were two decades ago, enabling researchers to simultaneously examine the effect of many different types of variables. More importantly, comparative analysis has seen the advent of techniques to tease apart correlated characters that are a result of shared phylogenetic history from those that are adaptive responses to similar environments. These statistical tools have resulted in our ability to draw out emergent patterns of behavior and morphology that distinguish migratory taxa from ecologically similar or related resident species. For example, adaptations that promote long-distance flight clearly provide constraints on trophic adaptations and related bill and hind-limb morphology (Winkler and Leisler, Chap. 7). The patterns that emerge from these broad comparative approaches should certainly inform the development of more focused experimental tests of function.

Demography and Life History

Demographic data, in particular, are crucial to answering key questions such as when in a migratory species' life cycle do population limitation and regulation occur and what

are the life history trade-offs involved in the evolution of migration (Runge and Marra, Chap. 28, and Sillett and Holmes, Chap. 32). Life history data are also becoming increasingly important to address the conservation needs of migratory species. Our understanding of the population biology of migratory birds has grown from an increase in studies of marked populations as much as—perhaps more than—from any particularly theoretical development. These studies, particularly those carried out over many years, provide necessary fodder for the development of theory in the field. For example, the intriguing question of why birds migrate as far as they do (to the point that northern populations “leap-frog” over the winter range of more southerly breeding populations) has inspired some sophisticated models (Bell, Chap. 4) that require much more detailed demographic data to test.

We are beginning to see studies of populations of migratory species with uniquely marked individuals during the nonbreeding season and a few studies (too few) of species that encompass populations at both ends. The estimation of survival and reproductive output is increasingly gaining prominence in studies of migratory bird ecology. New statistical techniques for estimating survivorship and reproductive success have moved the field forward in the past decade. Estimating and untangling juvenile survivorship and natal dispersal remain the greatest methodological challenge to developing a complete picture of the demography of migratory species. Winkler (Chap. 30) reviews a number of promising approaches to the study of dispersal in migratory birds; most evidence still appears to support the notion that migratory birds tend to have longer dispersal distances and that this results in more open and less differentiated local populations.

NEW PERSPECTIVES

Cross-Seasonal Approaches Are Necessary

We believe that the single most profound epiphany in the study of migratory birds is that their life histories and adaptations simply cannot be understood through increasingly detailed studies in a single season. Although this idea is not completely new, the degree to which it has permeated the thinking of ornithologists studying migratory species represents a clear paradigm shift that is reflected in all of the contributions to this volume. The contributions on morphology, cognition, foraging behavior, population biology, macroecology, and evolutionary processes (such as speciation) all underscore the fact that we need to integrate the effects of the different phases in the life of migratory birds to achieve a holistic understanding of each of these topics.

For example, early research examining the role of natural selection in shaping life histories and adaptations in migrants analyzed it as two competing hypotheses: either the breeding season is critical or the winter is. It should be clear that for a migratory bird to reproduce successfully—the

hallmark of evolutionary success—it must possess a phenotype that functions in all seasons. This will almost invariably result in a convex fitness set, where traits are not specialized for one particular season or habitat, but instead function successfully at all seasons. This generally requires adaptive compromises for any one season that can only be understood by examining how things work at all seasons. Price and Gross (Chap. 27) provides an intriguing example of how the ecological niches of *Phylloscopus* warblers are constrained across seasons.

Adaptive compromise is a critical theme in understanding various specific adaptations in migratory birds. For example, studies in this volume of external morphology (Winkler and Leisler, Chap. 32), physiology (McWilliams and Karasov, Chap. 6; Holberton and Dufty, Chap. 23), energy storage and management (Rogers, Chap. 9) are beginning to show how we can integrate selection through the annual cycle to understand adaptation in migratory species. Of course, the need to be successful in the face of changing conditions across the calendar is not unique to migratory birds, but can be found in all birds facing seasonal environments. Migratory birds are, therefore, a model system for studying adaptation in seasonal environments—an issue of general biological significance. Webster and Marra (Chap. 16) provide clear evidence that it is critical to understand the contribution of selection in different seasons and that events in one season can carry over to another. The importance of carry-over effects is modeled by Runge and Marra (Chap. 28) and show that competition for resources during the winter expresses itself in differential reproductive success on the breeding grounds thousands of kilometers away.

It is completely clear that ecological decisions made in one season are integrated into the selective factors shaping other necessary activities at other times in the annual cycle. The tools of cognitive ethology and comparative psychology are just beginning to be applied to learning how individuals acquire and use information during and between migratory excursions (Mettke-Hoffman and Greenberg, Chap. 10). A more holistic approach to the annual calendar must go beyond considerations of winter and summer events (two worlds) to include all time-sensitive activities. Constraints on where and when birds must migrate to optimize resources and flying conditions along the way certainly affect the choices birds make during the more stationary periods of their annual cycle. Data are beginning to confirm that migration is a time of year that accounts for much of the mortality (Sillett and Holmes, Chap. 32) and influences the condition of individual birds as they face the breeding season (Moore et al., Chap. 20, and Piersma et al., Chap. 21). As a consequence, we are beginning better integration of migration studies with our understanding of life history and demography as a whole. However, because individuals are hard to follow for extended periods, migration research requires additional innovative approaches to make major advances. As little as we know about how the period of migration affects the overall life history of migratory birds, the transition periods—such as the period immedi-

ately following breeding—are even more mysterious. Rohwer et al. (Chap. 8) reveal the richness of strategies influencing where and when to complete molt, arguably the most critical of the post-breeding activities. A thorough understanding of when and where birds molt is not only important in its own right, but is critical for using isotopes in feathers (see below) to study migratory connectiveness.

Migration, Speciation, and Population Connectivity

The role of migration in influencing evolutionary divergence of populations has long been an area of speculation (Salomonsen 1955). Generally, this thinking has focused on the role of migration in increasing dispersal distances and gene flow between breeding populations—thus inhibiting genetic divergence. Additionally, selection during the nonbreeding season may counter any selection for local adaptation that occurs when populations segregate in the breeding season. Such are the classic areas of inquiry into the evolutionary significance of migration. However, recent research has revealed other ways in which migration can influence the fundamental process of speciation. The study of migratory divides, which is exemplified in chapters by Irwin and Irwin (Chap. 3) and by Smith et al. (Chap. 18), suggest that geographically imposed migratory divides may select against hybrids and hence hasten the rate at which species form on either side of the divide. Migration may also contribute to speciation through a hypothesized “migration dosing,” as is proposed by Bildstein and Zalles (Chap. 13). They develop the argument that migrants blown off course (i.e., vagrants) may form the nucleus of populations that colonize islands and other isolated landforms. In the rare circumstance that these birds form stable reproductive populations, speciation may eventually occur. In summary, migration appears, at least theoretically, able to either impede or facilitate speciation depending on the situation.

Such processes of speciation acting primarily on breeding areas have consequences on the distribution of migratory birds during the nonbreeding season. Webster and Marra (Chap. 16) outline a broad and important research agenda on population connectivity that needs to be addressed as we learn more about how breeding populations map onto winter distributions and vice versa. Because such mapping will allow researchers to pursue many different kinds of questions, we spent considerable space in this volume discussing the various tools for the job. These tools include the use of genetic markers, stable isotopes, and trace elements in bird tissues (Smith et al., Chap. 18, and Hobson, Chap. 19). With the tools available to characterize populations, we may soon be able to link performance between particular areas of the breeding and wintering grounds (given that such structure exists). Szép and Møller (Chap. 29) take this bold step by relating the survival of two swallow species between breeding seasons in Europe to satellite-determined data on the condition of rainfall-dependent vegetation across the African continent. Clearly, understanding

both within- and between-season population connectivity will provide a more accurate picture of what a “population” truly is for a migratory species.

Expanding Research in Time and Space

Ornithologists have come a long way in the past two decades in recognizing the importance of long-term climatic cycles and rare disturbance events in shaping the life histories of birds. This increasing emphasis on long-term events has been fueled by the inadequacy of equilibrium-based models for explaining real populations in natural ecosystems, as well as by the need to place human-caused change in its proper context. We have made real progress in demonstrating the role of known climatic events (such as the El Niño Southern Oscillation) in shaping the life history of migratory and nonmigratory birds (Sillert et al. 2000). And we now understand that disturbance factors, such as severe weather and fire, have probably affected migratory birds as much as periods of stasis have (Rotenberry et al. 1995). Taking an even broader view of environmental instability, Winkler (Chap. 30) makes a tantalizing suggestion that dispersal strategies of temperate zone birds may have been shaped by the historical loss and gain of large areas of appropriate habitat during the Pleistocene. The unit of study has been changing as well. Avian ecologists now recognize that “communities” the size of study plots do not necessarily represent the dynamics of populations that interact across vast areas of natural and human-influenced landscapes (Pulliam 1988). We have a long way to go before we can understand the dynamics of populations over the relevant landscape mosaic during both the breeding and nonbreeding seasons, but this should remain a research priority.

A Focus on Individuals

Recent advances in behavioral ecology have brought us a major shift in emphasis over the past two decades. The individual bird is now taking center stage in our efforts to understand the ecology and evolution of migratory birds. Accompanying this greater interest in the performance of individuals is an increase in our ability to track their fates. With radiotelemetry we are better able to examine the decision-making strategies of individuals at the local scale, and thanks to advances in technology in satellite telemetry capabilities for larger species, we can now track birds through entire migrations. Cochran and Wikelski (Chap. 22) elaborate on these advances and provide an exciting vision for our ability to track individuals from space over even greater distances.

Ornithologists often focus on measuring the abundance of individuals over space. However, aware that interpreting presence/absence data is fraught with problems, ecologists and conservation biologists are increasingly concerned with the actual fitness consequences of different ecological decisions. Although fitness itself is the measure of ultimate importance, for most organisms—particularly highly mobile

ones—fitness is almost impossible to measure. It is even more difficult to assess how any one aspect of the life history of a bird affects its fitness. So ornithologists are employing, and in some cases developing, new techniques to measure the condition of individuals that in all likelihood correlate with fitness itself. Fitness indices, such as hormone levels, mass changes, and immune responses, do indeed represent an advance from the past but must still be compared with more direct measures of fitness so that we can be certain of their utility.

The traditional view is that most migratory birds form pair bonds that facilitate cooperation between the sexes to raise young. Recently, the nature of the pair bond has been challenged in several different ways (Stutchbury et al., Chap. 24). First, genetic analyses have shown that in migratory songbirds, many pairs are not truly monogamous. The male that participates in the cooperative activities associated with the pair bond does not necessarily sire all of the young. This discovery has led to a rich line of research on what factors favor the occurrence of extra-pair fertilizations and which pair member is in control of the reproductive decisions. Second, several interesting facets of male-female dynamics during the nonbreeding season have been discovered. For example, the number of taxa where it is known that pair bonds are developed and maintained during the nonbreeding season has expanded. Classically, extra-seasonal pair bonds were thought to be restricted to a few groups of long-lived migratory species—such as waterfowl. Now we know that a scattering of songbirds also develop such bonds. However, the possibility that pair bonds are maintained between seasons needs further exploration. Also interesting is the recent evidence that males and females compete for resources during the nonbreeding season. Evidence thus far suggests that males are behaviorally dominant over females and that this has consequences for male survival. Not understood, however, is how this can act as an evolutionary stable strategy.

MISSING PERSPECTIVES

As comprehensive as we believe this book is, we cannot help thinking about the important topics that did not receive coverage. Some of these areas may prove to be critical in any future synthesis about the ecology and evolution of bird migration. We would therefore like to touch briefly upon some of the holes in the tapestry of this volume with the hope that mentioning these gaps will still inspire future research.

Plasticity in Migratory Programs

The role of genetic control versus developmental plasticity and environmental influence of the migratory program, and their interaction, is a subject that will loom large in any future discussion of the evolution of migration patterns. Research in the past two decades has established for some

species the importance of genetically controlled endogenous rhythms in migratory behavior that play a key role in establishing the timing and at least general features of the geography of migration. However, the facultative response of *Zugunruhe* and other components of the migration program have been confirmed only in short-distance migrants and one or two Palearctic migratory species. How individuals make their own unique migration decisions and respond to variation in the environment is an area for physiologist and cognitive ethologists to explore, but it has profound implications for how migration can be coupled with or decoupled from environmentally based selection. Furthermore, the responsiveness of hard-wired behaviors to selection is an area that is just beginning to be explored.

Such plasticity in avian migratory programs is evident at both the individual and population levels. It is likely that even the most spectacular long-distance journeys evolved through gradual stages from residency, to partial migration where only some individuals in a population migrate, to complete short-distance movements, and finally to long-distance migrations. Detailed study of populations displaying partial migration systems (Cristol et al. 1998) may provide insights into the trade-offs underlying all migration systems. Partial migration systems are not a focus of any of the contributions to this volume, but their study represents a continuing research opportunity.

The Role of Pioneers and Vagrants

When it comes to normal dispersal, we are just beginning to frame the right questions and develop the methodologies to approach such questions for migratory species (Winkler, Chap. 30). However, the role of individuals that disperse well outside of the “normal” range of a species—so-called vagrant birds—has not been investigated from an evolutionary or ecological perspective (but see Bildstein and Zalles, Chap. 13). While these individuals provide much of the sport for birders, the numbers in which they occur suggest that they may also play an important role in the long-term success of lineages of migratory birds. In the highly unpredictable and rapidly changing Quaternary and Holocene climates and biomes, birds that produce pioneering phenotypes may be ecological winners. The existence of extreme vagrants may be a highly visible endpoint to a gradient of hyperdispersal in Temperate Zone migratory birds. The ecological and taxonomic correlates of avian vagrancy may be an area of high-risk research with a large potential pay-off, but the possible role of vagrants in speciation (migration-dosing [Bildstein and Zalles, Chap. 13]) remains an important area of research and discovery.

From Orientation to Habitat Selection

Orientation mechanisms have inspired some of the most elegant experimental work in animal behavior and physiology. After decades of this research, however, we are still far from understanding how birds locate and choose particular

sites at either end of their migratory route and how they are able to retrace their trips so precisely. The prospect of tracking individuals opens up the possibility of developing greater understanding for the mechanisms by which particular habitat patches are selected.

FUTURE DIRECTIONS

The hallmark of success of any scientific field is the degree to which it attracts the best and brightest of the next generation of investigators. We believe that the understanding of how migratory behavior shapes the adaptations of birds is inherently fascinating. More generally, migration systems provide an excellent opportunity for examining how environmental challenges at different stages of a life cycle shape avian adaptations. New technologies, better natural history information, and new perspectives have reinvigorated the field of ornithology and, more specifically, migratory bird biology. Thus we believe that this volume, in each of its chapters, provides any young investigator a wealth of important and interesting questions to pursue. We offer the following additional questions as our take on what some of the most interesting challenges of the coming decades might be. Our hope is that when another symposium is organized in 10 years, we have a few answers and a new list of even more compelling questions.

1. How can we integrate phylogenetic hypotheses for the evolution of different clades with our increasing understanding of paleoenvironments in different regions? How much were the current migration systems shaped by deep (Tertiary) versus recent (Quaternary) events?
2. What are the likely ecological attributes of taxa that gave rise to migratory populations?
3. To what degree do density-dependent versus density-independent events during migration contribute to the population dynamics of migratory birds?
4. What factors determine seasonal population limitation and at what time of year are populations of migratory birds most limited?
5. What are the primary factors that regulate populations of migratory birds?
6. What are the trade-offs in foraging ecology and trophic adaptations in species that migrate between temperate and tropical habitats?
7. How do social interactions and dominance relationships in one season affect events in subsequent seasons?
8. What cognitive abilities distinguish migratory and non-migratory species?
9. How do breeding populations map onto winter distributions across migratory species and vice versa? What are the social and ecological factors that underlie these patterns?
10. To what degree do competitive interactions between migrant species and between migrant and resident species shape the distribution and habitat use of migrant species year round?
11. What ecological and climatic factors shape patterns of migration and determine the travel and stopover strategies?
12. How does migration contribute to evolutionary processes within species and to the formation of new species?
13. To what degree are the annual time activity budget and migration strategies genetically constrained and what is the importance of behavioral plasticity?

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