Integrative and Comparative Biology, volume 50, number 3, pp. 261–279
doi:10.1093/icb/icq013

SYMPOSIUM

Grand Challenges in Migration Biology

Melissa S. Bowlin,[1,*] Isabelle-Anne Bisson,[†] Judy Shamoun-Baranes,[‡] Jonathan D. Reichard,[§] Nir Sapir,[¶] Peter P. Marra,[†] Thomas H. Kunz,[§] David S. Wilcove,[||] Anders Hedenström,[*] Christopher G. Guglielmo,[#] Susanne Åkesson,[**] Marilyn Ramenofsky[††] and Martin Wikelski[‡‡]

[*]Department of Biology, Theoretical Ecology, Ecology Building, Lund University, Lund, Sweden 22362; [†]Smithsonian Migratory Bird Center, National Zoological Park, PO Box 37012, MRC 5503, Washington, DC 20013-7012, USA; [‡]Computational Geo-Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94248, 1090GE Amsterdam, The Netherlands; [§]Center for Ecology and Conservation Biology, Department of Biology, Boston University, Boston, Massachusetts, USA; [¶]Department of Evolution, Systematics and Ecology, Movement Ecology Laboratory, Alexander Silberman Institute of Life Sciences, Edmond J. Safra campus, The Hebrew University of Jerusalem, Giv'at Ram, Jerusalem 91904, Israel; [||]Woodrow Wilson School and Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA; [#]Department of Biology, Advanced Facility for Avian Research, University of Western Ontario, London, Ontario, Canada N6A5B7; [**]Department of Biology, Animal Ecology, Ecology Building, Lund University, SE-223 62 Lund, Sweden; [††]Neurobiology Physiology Behaviour, University of California, Davis, CA 95616, USA; [‡‡]Department of Migration and Immuno-Ecology, Max Planck Institute for Ornithology, Schlossallee 2, D-78315 Radolfzell, Germany

From the symposium "Integrative Migration Biology" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2010, at Seattle, Washington.

[1]E-mail: melissabowlin@gmail.com

Synopsis Billions of animals migrate each year. To successfully reach their destination, migrants must have evolved an appropriate genetic program and suitable developmental, morphological, physiological, biomechanical, behavioral, and life-history traits. Moreover, they must interact successfully with biotic and abiotic factors in their environment. Migration therefore provides an excellent model system in which to address several of the "grand challenges" in organismal biology. Previous research on migration, however, has often focused on a single aspect of the phenomenon, largely due to methodological, geographical, or financial constraints. Integrative migration biology asks 'big questions' such as how, when, where, and why animals migrate, which can be answered by examining the process from multiple ecological and evolutionary perspectives, incorporating multifaceted knowledge from various other scientific disciplines, and using new technologies and modeling approaches, all within the context of an annual cycle. Adopting an integrative research strategy will provide a better understanding of the interactions between biological levels of organization, of what role migrants play in disease transmission, and of how to conserve migrants and the habitats upon which they depend.

Introduction

Migration is a common phenomenon in eukaryotes. It is the consequence of complex interactions between intrinsic factors (genetics, physiology, and behavior) and extrinsic factors (weather, habitat conditions, food availability, predation, topography; Åkesson and Hedenström 2007). It has evolved repeatedly and independently, in groups as diverse as slime molds, crustaceans, fish, amphibians, insects, reptiles, birds, and mammals (Bonner et al. 1953; Dingle 1996; Alerstam et al. 2003), and it can evolve quite rapidly (Able and Belthoff 1998; Alerstam et al. 2003; Bisson et al. 2009a). For these and many other reasons, we can use the phenomenon of migration to meet the five grand challenges in organismal biology identified by Schwenk et al. (2009): (1) understanding organismal responses to the environment, (2) using the functional diversity of organisms, (3) integrating living and physical systems, (4) understanding how genomes produce phenotypes, and (5) understanding how organisms trade-off stability and change.

Advanced Access publication April 21, 2010

The relationship between the first challenge and migration is straightforward: in order to migrate successfully, animals must respond appropriately to environmental cues and interact appropriately with both abiotic and biotic factors in their environment. As to the second, there is a great deal of functional diversity in migratory behavior; animals range from completely sedentary to altitudinal or partial migrants to short-distance, medium-distance, long-distance, and extremely long-distance migrants. Migration biologists also need to integrate living and physical systems in order to understand migration, because weather conditions and oceanic currents can influence migrants (Kunz et al. 2008) and because appreciating migratory locomotion necessitates a thorough understanding of biomechanics. As to the fourth challenge, little is known about the genetics underlying the behavior and physiology of migration, but that is gradually changing (Bensch et al. 2002, 2009; Berthold 2003); we encourage further research in this area. Finally, what we know about the evolution of migration suggests that it is an excellent system in which to study the interplay between stability and change. Thus, researchers who study migration have the opportunity to elevate organismal biology as a discipline and to help reach all of the goals outlined by Schwenk et al. (2009)—but, we would argue, only if they adopt an integrative research strategy. Employing such a strategy will also allow us to address some of the grand challenges in migration biology.

The grand challenges in migration biology

The primary goal of researchers who study migration is to understand when, where, why, and how animals migrate (Alerstam et al. 2003; Wilcove 2008). We intend to explore all the factors involved, ranging from the underlying genetics to the environmental conditions that drive animal movements (Nathan et al. 2008). We also wish to understand how migration affects individual survival and reproductive success, and ultimately how these factors affect, or are affected by, population demographics and the evolution of different life-history strategies. Understanding the effects of migrants on their breeding, wintering, and stopover areas is an equally poignant goal in migration research because these effects can be substantial (Holland et al. 2006a); spawning salmon, for example, transfer many tons of biomass each year from ocean ecosystems to terrestrial ones and historically transferred many more (Gresh et al. 2000). Furthermore, migratory movements may have far-reaching ramifications for other animals, including humans, because migratory animals have the potential to spread emerging diseases to new geographic areas (Liu et al. 2005; Li et al. 2005; Olsen et al. 2006).

The answers to these questions are important from a scientific standpoint, but they will also help us determine how best to conserve migratory populations. Many populations of migrants are declining, others are becoming more sedentary, and still others may not be able to adapt to rapid climatic change and alterations in habitat (Newton 2008; Wilcove and Wikelski 2008; Wilcove 2008). Therefore, we are also interested in how migrants are affected by their environments—especially because humans are currently fragmenting or destroying migrants' habitats, exploiting some migratory populations, depleting resources, altering the aerosphere (Kunz et al. 2008), and changing the climate. As Denny and Helmuth (2009) argued, one of the major obstacles to our ability to predict the effects of climatic change on organisms is an understanding of the ecomechanical and physiological consequences of such change; this is no less true for migrants. Much of the research on animal migration to date has focused on birds, but even within this clade, many questions remain to be answered. To answer these questions—and meet the grand challenges in organismal and migration biology—we must adopt an integrative research strategy.

Integrative migration biology

By "integrative research," we mean conducting activities that involve multiple taxa, the complete annual cycle of organisms, multiple scientific disciplines, and conservation efforts. This type of research also incorporates traditional and novel technologies and modeling techniques, and it combines laboratory-based studies and field-based studies to take full advantage of what each approach has to offer, similar to the strategy outlined by Pennycuick (1998) for research into bird flight. Of course, it is impossible for a single project to fully integrate all aspects of migration biology, but new insights can emerge if we incorporate even one additional methodology or scientific discipline into a given research project. Below, we highlight some examples of integrated research on migration and demonstrate how this strategy has already begun to answer some important and pervasive questions.

Integrating across species and clades

Schwenk et al. (2009) argued that we should take advantage of biodiversity and investigate the different ways natural selection has solved various problems. Migration is one of several traits that animals have evolved to compensate for seasonality and/or temporally or spatially ephemeral resources. Indeed, environmental factors may influence migratory behavior more than phylogenetic relationships do, although characteristics of certain clades may have predisposed these animals to evolve migration (Fleming and Eby 2003). For example, swimming and flying have lower costs of transport per unit distance than terrestrial locomotion has (Schmidt-Nielsen 1972); taxa that swim or fly consequently are particularly prone to evolving migratory behavior (Alerstam et al. 2003).

Research on many different migratory species has led to a better understanding of the underlying patterns of migration and has provided general hypotheses about the ecology and physiology of migrating animals (Dingle and Drake 2007). These kingdom-wide comparisons are particularly important as we explore the ecology and physiology of migrating animals using modern methods and technologies that make it possible to follow animals both directly and indirectly throughout an increasing fraction of their lives (Fuller et al. 2005; Hobson 2007; Kunz et al. 2007a; Klaasen et al. 2008; Holland and Wikelski 2009). Inter-taxon approaches are also important when exploring the consequences of environmental change, because such changes are likely to affect multiple migratory clades and have similar effects on them (Kunz et al. 2007a, 2007b; Wilcove and Wikelski 2008). Finally, migration often involves a diversity of species; rarely does a single species move by itself. As a result, transfer of information both intraspecifically and interspecifically can occur during migration (Muhkin et al. 2005; Couzin et al. 2005). For all these reasons, we need to include multiple taxa in our research programs.

The challenges associated with long-distance movements are common to most migrants, and as a result many of them have evolved similar physiological and morphological adaptations, usually convergently. Energy balance during migration is critical, particularly during locomotion; for example, regional heterothermy of the wings of bats may help to reduce the costs of maintaining euthermic body temperature during prolonged nighttime flights (Reichard et al. 2010). Bats in the family Molossidae have a highly vascularized hairless region (a thermal window) under their wings that facilitates thermoregulation during flight (Reichard et al. 2010). Similarly, some birds are able to position their uninsulated legs appropriately for heat dissipation or conservation depending on their physical exertion and the air temperature (Torre-Bueno 1976; Bryant 1983). Such adaptations for flexibile, context-dependent thermoregulation presumably optimize the use of limited reserves of water and energy during migration.

Understanding the intricacies of migration can be especially challenging for small and long-ranging species. Thus, developing models and methods for these species relies on synthesizing findings and methodologies from studies on other taxa. Protocols for investigating migration using stable isotopes, for example, were developed and initially tested in avian (Marra et al. 1998) and marine species (Killingley 1980), but are now routinely employed in mammals, fish, amphibians and reptiles (reviewed in Hobson 2007; Hobson and Wassenaar 2008; Cryan and Diehl 2009). A critical component of using stable isotopes to track animal migrations is understanding how they fractionate across trophic levels. Thus, as research uncovers stable isotope relationships with the environment in one taxon, those who study the predators or prey of that animal can gain critical information about the sources of input of stable isotopes (Fleming et al. 1993; Fleming 1995; Sullivan et al. 2006; Hobson and Wassenaar 2008). Similarly, small data loggers that had been previously used on ocean-going migrants (Gonzalez-Solis et al. 2005) are now being applied to small terrestrial migrants (Stutchbury et al. 2009). Applying new (and old) methodologies to an increasing variety of migrants will help us understand, among other things, how a life-history strategy like migration can evolve in so many different taxa and what its costs and benefits are.

Integrating within a species

Selecting a model species to study migration can also prove highly fruitful, especially when expertise can be built up by a research group (or groups), with new researchers adding more knowledge about specific aspects of the migratory system or species being studied. Such long-term knowledge and expertise will, over time, naturally lead to integrative studies, combining knowledge about different parts of the system to improve our understanding not only of the entire migration process, but, for example, how it connects to other life-history traits and its potential relevance for conservation. Unfortunately, we do not have the complete genome sequence of any migratory species, although efforts are underway to obtain sequences for the little brown bat (*Myotis lucifugus*) (http://www.broadinstitute.org/science/projects/mammals-models/mammalian-genome-project). We therefore suggest that some of the next genetic model organisms (discussed by Satterlie et al. 2009) include migratory model organisms.

A prominent example of one such species is the red knot (*Calidris canutus*). This species has been studied for decades and, as a result, a large body of information has accumulated on its stopover ecology, refueling rates, flight energetics, physiology, importance of wind for use of stopover sites, and much more (Dick et al. 1987; Wiersma and Piersma 1994; Kvist et al. 2001; Baker et al. 2004; Piersma et al. 2005; van Gils et al. 2006; Dietz and Piersma 2007; Dietz et al. 2007; Leyrer et al. 2009; Shamoun-Baranes et al. 2010b). Over the years, these studies have incorporated observations and measurements of red knots in the field, samples of food resources, laboratory experiments, and modeling. This rich body of information provides valuable insight into this particular migratory system, collectively enabling researchers to work towards understanding seasonal interactions and linking individual responses to population-level patterns. Unfortunately, this knowledge was not enough to prevent a major population crash of the red knot in North America (see Conservation section, below; Niles et al. 2009), but it can perhaps help us determine how best to help this population recover.

Integrating the annual cycle of organisms

A third strategy that researchers can use to address the grand challenges in migration biology is, perhaps paradoxically, to focus on other life-history stages. The mere fact that many migratory species spend substantial amounts of time and energy each year in two or more widely separated geographic areas and shorter periods at multiple stopover sites while en route has obvious, but poorly-studied, consequences for all aspects of their biology. The conditions and selective pressures at winter locations are likely to affect individual condition and performance during spring migration and during the breeding season and vice versa (McNamara et al. 1998; McNamara and Houston 2008). This fact has important implications for the ecology, evolution, and conservation of seasonal migrants. Periods of the annual cycle are inextricably linked, such that ecological circumstances within one season may influence events in subsequent seasons, a phenomenon referred to as a *seasonal interaction* (Ramenofsky and Wingfield 2006; Wingfield 2008; Hahn and MacDougall-Shackleton 2007; Marra and Studds 2010).

Seasonal interactions can operate at the individual or population level (Fleming and Eby 2003; Newton 2004; Webster and Marra 2005; Runge and Marra 2005; Norris 2005; Marra et al. 2006). At the individual level, effects such as poor physical condition or late arrival carry-over from one season to the next and can thus generate ecologically relevant variation in a life-history attribute in a later season. Empirical evidence for such effects in migratory animals has been strongest in non-passerine birds, including waterfowl (Heitmeyer and Fredrickson 1981; Mihelsons et al. 1985; Kaminski and Gluesing 1987; Bêty et al. 2004) and shorebirds (Goss-Custard et al. 1995a, 1995b; Gill et al. 2001), but evidence is also mounting for the importance of seasonal interactions in passerine migrants (Marra et al. 1998; Sillett et al. 2000; Bearhop et al. 2004; Saino et al. 2004; Smith and Moore 2005). These studies have focused on understanding how the annual cycle influences condition and population abundance, but more recent studies have also examined how seasonal interactions can influence phenomena such as natal dispersal (Studds et al. 2008) and sexual selection (Reudink et al. 2009).

Seasonal interactions can also involve mortality within a season but act at the population level to influence density-dependent effects across seasons. This has been demonstrated most clearly in the context of hunting mortality in winter and whether it is additive or compensatory with other sources of mortality in waterfowl (Gauthier et al. 2001; Frederiksen et al. 2001; Lebreton 2005). The evidence supporting the importance of population-level seasonal interactions in passerine migrants is scarce (Sillett et al. 2000; Stokke et al. 2005), but this is likely a demonstration of the difficulty of obtaining such data rather than a testimony against such interactions.

Modeling the annual cycle and comparing model predictions to measurements provides an opportunity to assess the interactions and carry-over effects between different aspects of migration (McNamara et al. 1998; Pettifor et al. 2000; Klaassen et al. 2006; Barta et al. 2008; Bauer et al. 2008). Doing so also allows us to examine the fitness consequences of different behavioral decisions, particularly under varying environmental conditions. However, we need better estimates of various sources of mortality throughout the annual cycle in migrants, whether such mortality results from density-dependent, age-related, or geographically-dependent effects (Strandberg et al. 2009).

Another obstacle to understanding seasonal interactions is a lack of knowledge about migratory connectivity, or the geographic linkage of individuals or populations between different stages of the annual cycle (Webster et al. 2002). Currently, migratory connectivity is poorly understood in most species, yet this variable is essential for interpreting fundamental ecological and evolutionary phenomena (Lawton and May 1983) and for developing effective conservation strategies. Recent advances in tracking migratory birds using satellite transmitters, GPS loggers, small light level loggers (geolocators), DNA markers, and stable isotopes all represent potential approaches for tracking migratory animals throughout the annual cycle (Kunz et al. 2007b; Holland et al. 2009; Robinson et al. 2010). The continued development of such approaches is essential to our ability to understand the biology of migratory animals in the context of the annual cycle, which will aid in our ability to understand organism–environment linkages (Schwenk et al. 2009).

Integrating laboratory-based and field-based work

Another strategy we can use to develop a more complete understanding of migration is to combine field-based and laboratory-based studies (Gwinner 1973). Many important advances in migration biology have their origins in measurements of variables (such as heart rate or heat loss) under field conditions that have only previously been measured in the laboratory (Butler et al. 1998; Bowlin and Wikelski 2008; Reichard et al., 2010), or studying animals under controlled laboratory conditions (Lindström et al. 2000; Hasselquist et al. 2007). Measurements in the field make it possible to observe the behavior and physiology of animals in the environment in which natural selection acts upon them, whereas measurements in the laboratory make it possible to manipulate variables that cannot be controlled in the field. By combining these two approaches, we can achieve a more complete understanding of the particular aspect of migration under investigation.

Avian orientation provides an excellent example of how a single field study helped to clarify the conflicting results of many laboratory-based studies. Early integrative migration biologists had demonstrated that migratory birds have the ability to use many different cues to orient, such as polarized light (Able 1982), geomagnetism (reviewed in Wiltschko and Wiltschko 1995), and the stars (Sauer 1957; Emlen 1975). To determine which of these was the primary cue that birds use to orient, migration biologists conducted multiple 'cue-conflict' experiments with primarily captive animals (Åkesson 1994). In these experiments, birds placed in orientation cages were exposed to cues that 'pointed' in different directions and researchers observed their orientation. Unfortunately, the results of these experiments were ambiguous (see Åkesson 1994; Muheim et al. 2006a for reviews); sometimes it appeared that birds recalibrated a celestial compass based on magnetic cues, and other times it appeared that they recalibrated their magnetic compass based on celestial cues.

Cochran et al. (2004) conducted a field study designed to determine which cues free-flying birds use during migration. Thrushes were fitted with radio-transmitters and exposed to an altered magnetic field at sunset; they were then released and followed as they migrated naturally. Results were consistent with the hypothesis that these birds had recalibrated their magnetic compass based on the position of the sun at sunset or on associated patterns of polarized light. Prior studies on cue-conflicts yielded confusing results because the animals were exposed to the sunset prior to tests in some experiments, particularly those conducted during the pre-migratory period, but not in others (Muheim et al. 2006a). Subsequent experiments on captive birds confirmed that several additional species also recalibrated their magnetic compasses when afforded a view of the horizon at sunrise and sunset, but were unable to do so when they did not have a view of the horizon (Muheim et al. 2006b, 2007, 2009). Recent evidence suggests that bats might also use a sunset-calibrated magnetic compass (Holland et al. 2006b, in press).

Field-based studies have also revealed the importance of physiological state (e.g. Sandberg 2003 for review), topography (Åkesson 1993, 1999; Åkesson et al. 1996a; Zehnder et al. 2002), timing of migration (Åkesson et al. 1996b), and weather (Åkesson and Hedenström 2000; Åkesson et al. 2002; Wikelski et al. 2006; Chapman et al. 2010) on the orientation and migratory decisions of birds and insects. Such studies clearly show the need to be aware of the physiological state of the animal as well as the external conditions it experienced prior to capture when interpreting results from experiments with caged migrants.

Notwithstanding, laboratory-based studies should not be abandoned: Cochran et al.'s (2004) field study may have provided the original impetus for a paradigm shift in avian orientation, but some variables are difficult, if not impossible, to manipulate in the field. For example, no method can rotate the stars in new directions while a bird is migrating naturally, nor can changes in magnetic fields or polarized light patterns be made during natural migratory flight without specialized, potentially cumbersome equipment. Thus, further studies on captive birds will be needed before we can understand, among other things, the exact mechanism(s) behind the recalibration of the magnetic compass revealed by Cochran et al. (2004).

Integrating theoretical models

Pennycuick (1998) argued that, in addition to field observations and laboratory-based studies, we need theoretical models to completely understand bird flight; the same is true for animal migration. Indeed, the study of migration ecology rests on a solid theoretical foundation based on biomechanics and concepts of optimality (Alerstam and Hedenström 1998). These theoretical concepts mainly concern the process of migration by an individual animal, considering such variables as duration of stopover, timing of departure from stopover sites, optimal fuel loads at departure, migration step length, migration routes, and the overall speed of travel (Hedenström 2008). In a broader sense, models of the annual routines of migrants, which use multiple variables for the state of individuals and dynamic programming (Barta et al. 2008), and seek the best possible timing of major events (breeding, molt, and migration) in a seasonal world, also fall within the domain of migration theory. All of these models represent attempts to integrate living and physical systems, as prescribed by Schwenk et al. (2009).

A fundamental component of simple optimality models is the "range equation" (Alerstam and Hedenström 1998), which gives the potential flight range based on a specified amount of metabolizable energy (fuel). The equation will vary depending on the type of migration (flying, swimming, or running/walking), but the overall characteristic of the model is a diminishing return function, meaning that the increase in range from a certain amount of fuel decreases as fuel load increases. Thus, migrants must trade off the benefits of additional fuel, such as increased range and higher safety margins, with the energetic costs of carrying the fuel.

Working out predictions about optimal tactics requires assumptions about some relevant surrogate currency, which can be energy, time or survival rate. It is assumed that by optimizing such an immediate currency, or a combination of two or more simple currencies, the animal also maximizes its fitness. In most cases, however, it is not possible to measure fitness directly in migratory animals, but by assuming a particular currency and an appropriate decision rule, it is possible to predict an optimal behavior, for example the duration of stopover and the associated fuel load at departure as a function of the rate of fuel deposition (Lindström and Alerstam 1992). In doing so, relevant constraints must be considered, such as the physiological capacity for digesting food. To experimentally test whether migrants respond to variation in fuelling rates, one could provide additional food at a stopover site and monitor individual mass (fuel) gain and timing of departure (Lindström and Alerstam 1992). A number of such experiments have been conducted and have confirmed the predicted positive relationship between fuelling rate and the fuel load at departure (reviewed in Hedenström 2008). These studies support the hypothesis that minimization of time is an important strategy in avian migration.

By considering the rate of energy intake and the power required for locomotion, the overall speed of migration (including both fueling and active migratory locomotion) can be derived and how it scales with body size can be determined (Hedenström and Alerstam 1998; Hedenström 2003). Theory predicts that the overall rate of migration should decline with increasing body size, which is consistent with observational data. However, some recent studies in which migration speeds were measured in passerines (Stuchbury et al. 2009) and the arctic tern *Sterna paradisaea* (Egevang et al. 2010) seem to surpass the expected rates. It is unclear at this stage if this discrepancy is due to the use of beneficial winds, if physiologists have misjudged the capacity of migrants for fuelling, or if other aspects of the theory need to be refined.

For migratory birds, bats, and insects, mechanical flight theory also predicts different optimal flight (air) speeds depending on ecological context (Norberg and Rayner 1987; Norberg 1990; Hedenström and Alerstam 1995). The cruising speed of flight during migration should be either the maximum range speed (energy minimization), or a speed slightly faster than this (time minimization), both of which are significantly faster than the speed of minimum power. The exact calculation of these alternative speeds is difficult; hence a powerful test to see if animals do adjust their flight speeds according to theory is to compare speeds of the same species in contrasting situations, such as migration versus display flight (Hedenström and Alerstam 1996), or commuting versus food searching (Grodzinkski et al. 2009). What emerges from such comparisons is that birds and bats do adjust speed adaptively according to context.

It is important to keep in mind that migrating animals are not always able to behave optimally. Cochran and Wikelski (2005) showed that nocturnal avian migrants can sometimes be pushed backward against their normal migratory direction by headwinds but will still fly for hours in such winds. These birds presumably behave in this sub-optimal way because they use simple decision rules to guide their take-off decisions and flight times (Cochran and Wikelski 2005). On average, such rules are presumably beneficial (Wikelski et al. 2006), and are therefore maintained by natural selection, but these rules can have negative consequences for some individuals.

Integrating other biological disciplines

As Pennycuick (1998) pointed out, we need empirical observations to complement theoretical predictions. A great deal of migration research has focused on behavior and ecology, but a complete understanding of migration requires data from other biological disciplines. Below we discuss two of many possible examples of integrating additional biological disciplines.

Physiology

Physiology brings a distinct mechanistic and constraint-oriented perspective to the study of migration. Because migratory movements have such high physiological demands, much of the behavior and ecology of migrants, as well as the evolution of their migration strategies, can be understood by studying the physiological and biochemical mechanisms that influence migration performance. In other words, physiologists emphasize the need to answer proximate “how” questions to fully answer the ultimate “why” questions.

Two of the greatest physiological challenges to migrants are the optimal accumulation and budgeting of energy and nutrients needed to fuel movement. For example, several years at sea are required for semelparous salmon (*Onchorynchus sp.*) to accumulate nutrient stores for their all-or-none migration and spawning. Similarly, monarch butterflies (*Danaus plexippus*) must carefully budget their fuel stores to be able to migrate in the autumn, over-winter, and migrate again the following spring, and many temperate bat species must deposit sufficient energy reserves (i.e. fat) in the autumn to sustain physiological processes through hibernation and then migrate to summer ranges before insect prey become available (Kunz et al. 1998). As discussed above, the rate of utilization of fuel during flight, the rate of fuel deposition at stopover, and the delay between arrival and net refueling (search/settling time) are key parameters in optimal migration models (Alerstam and Hedenström 1998; Engel et. al, this volume), all of which have a sound physiological basis.

The rate of utilization of fuel during locomotion is influenced by a number of factors including morphology, speed of movement, and the conditions in, and attributes of, the media traversed (e.g. wind speed and turbulence for airborne animals; Bowlin and Wikelski 2008; Pennycuick 2008). Notwithstanding, the physiological mechanisms governing the mobilization, transport, oxidation, and ultimately conversion to mechanical power of fuel have an overriding influence on the duration of flight by affecting metabolic efficiency and the rate of use of different stores (e.g. fat and protein). Laboratory and field studies of how these mechanisms function, how they are regulated, and how intrinsic (e.g. age and sex) and extrinsic (e.g. diet, photoperiod, altitude, temperature, and humidity) factors influence them are critical to understanding flight and, ultimately, migration performance.

Studies of the physiological aspects of search/settling time and refueling rate also exemplify how laboratory and field studies can be integrated to shed light on the ecology and evolution of migration and inform conservation efforts. It has often been observed that birds do not gain weight for one or more days following arrival at stopover sites, but it was unclear whether this search/settling behavior reflected time required to find the best feeding conditions, or a period of physiological recovery (Klaassen and Biebach 1994; Alerstam and Hedenström 1998; Guglielmo et al. 2001). In recent years, data from the field and laboratory have revealed that migrants catabolize significant amounts of lean tissue during flight, particularly from the digestive system, and thus must rebuild this digestive capacity before they can increase their refueling rates (Åkesson et al. 1992; Klaassen and Biebach 1994; Piersma et al. 1999; Karasov and Pinshow 2000). Settling time could also be affected by other physiological requirements, such as the repair of damaged flight muscles (Guglielmo et al. 2001) or recovery from sleep deprivation (Schwilch et al. 2002). In optimality models, search/settling time is generally treated as constant for a given simulation, yet the physiological information suggests that it may be positively related to the duration of the previous flight; long flight may cause greater catabolism and fatigue or injury of muscles. This potential interplay between duration of flight and subsequent search/settling time should be explored further.

Even after accounting for post-flight recovery and major ecological factors (e.g. availability of food, predation risk, and competition), refueling rate will be strongly influenced by physiological processes because food must be digested, absorbed and reassembled into functional tissues or energy stores. Moreover, the macronutrient and micronutrient composition of the diet can influence flight performance and fuel mixture (Gannes 2001; Pierce et al. 2005; Price and Guglielmo 2009; Weber 2009). Thus, to fully understand what nutrients migrants seek at stopover sites, and to develop conservation strategies to provide these resources, we need to identify the mechanisms of digestion and post-absorptive processing of nutrients underlying the deposition of fuel and which set limits on refueling rate (Lindström 1991; McWilliams and Karasov 2001).

Denny and Helmuth (2009) provided several excellent examples of how biomechanical and physiological studies can aid conservation efforts. For migratory animals, conservation efforts are being facilitated by the development of new physiological approaches to assess rates of refueling in birds (Guglielmo et al. 2005) and bats (McGuire et al. 2009). Feeding/fasting states are reflected in the concentrations of key metabolites in plasma, and numerous laboratory and field studies show that rate of change in mass of individuals sampled only once can be estimated from metabolite profiles (Jenni-Eiermann and Jenni 1994; Guglielmo et al. 2005; Cerasale and Guglielmo 2006). This is an advance over other methods of assessing refueling rate, such as analysis of recapture data or relationships between capture mass and time of day, because every captured individual provides useful data (Guglielmo et al. 2005). By combining this simple approach with other standard methods (e.g. morphometrics, population censuses, mark-recapture analyses, telemetry, behavioral observations, surveys to assess food availability, and stable isotope analyses), it is now possible to study how factors such as age, weather, and habitat structure affect individual deposition rates of fuel. We can potentially improve conditions for migrants by providing high-quality stopover sites that allow migrants to rapidly replace depleted energy and nutrient reserves. Physiology can therefore play an important role in conservation by providing the means of identifying sites with suitable refueling conditions in addition to the role it may play in improving our ability to predict the ecological effects of climatic change (Denny and Helmuth 2009).

Many captive migrants express a suite of migratory behaviors, allowing researchers to study specific aspects of their physiology. For example, nocturnal avian migrants undergo normal daily fueling and activity cycles in the laboratory. Throughout the daylight hours, these birds feed, amassing fuel stores composed of primarily lipid and protein. At the close of the day, prior to nocturnal "departure," all activity ceases. This has been termed the *quiescent phase*, and is considered to be a transitional period when digestion is completed and various mechanisms are activated in preparation for departure. With the onset of darkness, captive birds exhibit flight-like activity (e.g. beating their wings, extending the beak skywards and attempting to take off). Such activity is termed "migratory restlessness" and continues until dawn, after which birds return to their daytime activities, including feeding and resting.

Researchers can take advantage of these behavioral changes to study the underlying hormonal changes and how they are affected by the environment, thus addressing the challenge put forth by Denver et al. (2009). Studies investigating the hormonal basis of captive migrants' diurnal rhythms find that plasma levels of the metabolic and behavioral glucocorticoid hormone, corticosterone, are elevated when birds are expressing migratory restlessness, suggesting that this hormone may play an important role during periods of high energy demand (Landys et al. 2006; Ramenofsky et al. 2008). During migratory restlessness, both proteins and lipids are mobilized, elevating uric acid and the ketone β-hydroxybutyrate. These findings corroborate results obtained from free-ranging migrants (Jenni-Eiermann and Jenni 1994; Guglielmo et al. 2005). However, the studies on captive migrants illustrate how rapidly the behavioral transitions occur in conjunction with endocrine and metabolic fluctuations, thus providing new insight into the behavioral and physiological capabilities of migrants. Although the exact mechanisms involved have yet to be discerned, the fact that captive migrants express a full range of migratory behavior means that researchers have a valuable model for investigating the physiological parameters of migratory behavior. Results from these investigations have offered new clues that researchers might have missed had only free-living migrants been studied (reviewed by Landys et al. 2006). Thus, employing this type of research strategy provides an exceptional opportunity for understanding the physiological mechanisms underlying the behavioral expression of migration.

Microbial ecology

While much attention has focused on the ecology, evolution and physiology of migrating animals, relatively little attention has been dedicated to understanding the diverse microorganisms that live on these migratory animals and how migration affects the dynamics of these microbial communities. Yet, microorganisms account for more than half of the total biomass on the planet (Nee 2004) and are key contributors to the health of most ecosystems (Madigan et al. 1996; Olff et al. 2009). Given the ubiquity (Waldenström et al. 2002) and importance of bacterial assemblages, the need to understand how they are acquired, transported, and dispersed across ecosystems is critical to the global understanding of the biosphere. We now know that animal migration can act as both an efficient mode of transport for microorganisms (Waldenström et al. 2002; Liu et al. 2005) as well as a catalyst for infection by endoparasites and viral pathogens (Gylfe et al. 2000). Moreover, with the emergence of zoonotic diseases such as avian influenza (Liu et al. 2005), West Nile virus (Marra et al. 2004), and severe acute respiratory syndrome (SARS; Li et al. 2005; Lau et al. 2005), animal migration has become a topic of multidisciplinary interest (Reed et al. 2003; Hubalék 2004; Calisher et al. 2006). Microbial ecology is therefore an appropriate component of integrative migration biology.

Avian plumage, for example, provides a particularly interesting microbial ecosystem. Feathers harbor a diverse microbiota (Burtt and Ichida 1999; Bisson et al. 2007), which includes bacteria and fungi. Microorganisms in the plumage of migratory birds are exposed to many different environments within a single annual cycle because the bird migrates between breeding and non-breeding sites and uses numerous stopover sites en route. Recent studies have indicated that local landscapes play a significant role in microbial acquisition by migratory birds. For example, the greater abundance of common soil bacteria (Lucas et al. 2003) in ground-foraging birds (Burtt and Ichida 1999) suggests exchanges between the microbiotas of soil and plumage. Indeed, Bisson et al. (2007) found that the composition of the bacterial assemblage in avian plumage varied between breeding and wintering sites, indicating that it may be possible to use microorganisms as tags in population connectivity studies if the microbial "signature" on the plumage remains informative throughout migration. The microbial community of avian plumage also varies in relation to migration strategy and stage of the annual cycle: resident birds differed significantly from migrants in the composition of the microbial communities of their plumage and Nearctic residents had higher microbial diversity than did Nearctic migrants (Bisson et al. 2009b). Moreover, the microbial composition of plumage differed significantly between fall pre-migratory stages and either breeding or non-breeding stages. Migration and season may thus play an important role in the dynamics of the microbial community in avian plumage, and may also affect the dispersal of pathogens.

Migratory animals can be highly mobile reservoirs for both pathogenic and non-pathogenic microorganisms. A fundamental understanding of how animals acquire and disperse microbes and the interaction between microbes and the local environment with which their hosts interact during migration will provide insights into the movement of microbes across the globe. Perhaps more importantly, studying the relationship between microbial ecology and migration may reveal how shifting migration patterns resulting from climatic change will affect when, where, and how migrants transport and disperse microorganisms, including invasive species such as the fungus associated with white-nose syndrome in hibernating bats (Gargas et al. 2009).

Integrating other scientific disciplines

Incorporating biological disciplines such as physiology and disease ecology into research on migration can greatly expand our understanding of the phenomenon. Incorporating other scientific disciplines may be equally useful; Schwenk et al. (2009) identified integrating living and physical systems as one of their grand challenges in organismal biology. Research on migration can help us address this challenge. Environmental conditions can influence migrants in numerous ways, resulting in instantaneous costs (or benefits) and more cumulative and even evolutionary consequences (Nathan et al. 2005; Shamoun-Baranes et al. 2010a). Specifically, because aerial, marine, and freshwater migrants move long distances through highly dynamic fluids, the properties of the medium may have multifaceted, direct consequences on their movement as well as indirect consequences on fitness. An example of a direct consequence is the effect of wind and water on the speed of progression during the journey (Chapman et al. 2010; Shamoun-Baranes et al. 2010a). To thoroughly investigate these consequences, as well as their dynamics at multiple scales, interdisciplinary research is essential. The emerging discipline of aeroecology, for example, promotes the integration of atmospheric science, earth science, geography, ecology, computer science, and engineering into a conceptual framework that focuses on where, when, how, and why organisms use the aerosphere (Kunz et al. 2008). Although most studies on the effects of environmental conditions on migrants do not explicitly integrate expertise in all fields simultaneously, they do require some basic knowledge from most of these fields; many of the best-known migrations, for example, occur in the aerosphere (Drake and Farrow 1988). From an ecological and evolutionary perspective, however, the aerosphere is one of the least understood substrata of the troposphere with respect to how organisms interact with, and are influenced by, this highly variable, fluid environment (Taylor 1986; Kunz et al. 2008).

One exception to this rule is that the evidence for strong effects of wind and other weather conditions on migrating birds (Richardson 1978, 1990; Liechti 2006; Shamoun-Baranes et al. 2010a), bats, and insects (Williams 1957; Srygley et al. 1996; Kunz et al. 2008) is diverse and widespread. For example, birds and insects typically depart under beneficial horizontal wind conditions (Åkesson and Hedenström 2000; Dänhardt and Lindström 2001; Åkesson et al. 2002; Chapman et al. 2010). Due to synoptic-scale correlation in weather conditions, extending over hundreds and possibly thousands of kilometers spatially, and over several days temporally, this coordination presumably benefits these animals throughout a major portion of their migration (Gill et al. 2005, 2009; Shamoun-Baranes et al. 2006). In addition to horizontal winds, the spatial and temporal distribution of vertical air currents can substantially affect the soaring of migratory birds (e.g. Shamoun-Baranes et al. 2003a) and insects (Reynolds and Reynolds 2009; Reynolds et al. 2009). Updrafts may limit the movement of soaring animals to locations and times when intense air currents exist, because these currents must be capable of lifting the animals to higher altitudes (Pennycuick 1972; Leshem and Yom-Tov 1996; Shannon 2002a, 2002b). Recent findings from European bee-eaters (*Merops apiaster*) that migrated over southern Israel (Sapir 2009), as well as earlier studies on several North American butterfly species (Gibo and Pallett 1979; Gibo 1981), suggest that the development of updrafts always precede the onset of movement. Intensity of updrafts and the height of the boundary layer influence the altitude at which several migrants soar (Shannon 2002a, 2002b; Shamoun-Baranes et al. 2003a, 2003b), and can positively affect the speed and progression of vultures during migration (Mandel et al. 2008). Although soaring flight is thought to be energetically inexpensive, moving through such turbulent air currents may induce elevated metabolic costs for flapping birds (Bowlin and Wikelski 2008; Cochran et al. 2008), presumably due to instabilities of flight. These studies demonstrate how important atmospheric dynamics are in space and time for aerial migrants. Evidence for hydrodynamic effects on marine migrants is scarcer, but from the several studies that considered such effects, they seem to be at least as influential (Luschi et al. 2003; Polovina et al. 2004; Gaspar et al. 2006).

To study environmental effects on long-distance migrants, one must consider the conditions encountered by the migrants throughout their extended migratory routes. Because atmospheric and oceanic measurements generally cannot be carried out at the same spatial and temporal scales at which they influence migration, the most practical way to explore how the dynamics of air and water affect the movement of migrating animals is by modeling the relevant processes (see Shamoun-Baranes, 2010a). Many studies have used robust meteorological models, such as the NCEP-NCAR re-analysis archives (Kalnay et al. 1996), which have a spatial extent on the order of an entire continent or even the entire globe, and a temporal extent of several tens of years, to investigate different properties of the movement of birds and insects (Thorup et al. 2003; Shamoun-Baranes 2003c; Erni et al. 2005; Stefanescu et al. 2007; Bowlin and Wikelski 2008; Mandel et al. 2008). The principal limitation of these models is their relatively poor spatial (several tens to several hundreds of kilometers) and temporal (several hours) resolution. Thus, the ability of these models to explain details of specific, highly variable properties of animal movements, such as flight strategy selection (e.g. flapping or soaring) and altitude, is relatively poor.

Shannon et al. (2002a, 2002b) and Shamoun-Baranes et al. (2003a, 2003b) pioneered the application of atmospheric simulations to the study of bird flight at local and regional scales, but these models are limited in the processes they modeled and in their spatial extents. When exploring fine-scale responses to meteorological conditions, we advocate the use of atmospheric and oceanic models such as the Regional Atmospheric Modeling System (RAMS; Pielke et al. 1992; Walko et al. 2000; Cotton et al. 2003) and the Ocean–Land–Atmosphere Model (OLAM; Walko and Avissar. 2008). These models have been used extensively in the atmospheric sciences to study events that occur anywhere from a tiny (cm) scale to a global scale (Alpert et al. 2006). The capacity of these models to simulate variable meteorological processes, ranging from synoptic (e.g. the dynamics of large pressure systems), to meso- (e.g. sea breeze circulation), to local (e.g. valley–mountain orographic flows) scales, permits researchers to investigate the movement of aerial migrants in fine detail over extensive areas. Recently, for example, simulations of this kind were conducted to help explain flight mode, flight speed, soaring height, and the extent of wind drift of migratory birds passing over southern Israel (Horvitz 2009; Sapir 2009).

Understanding how animals respond to, and are influenced by, environmental dynamics at various scales is an essential piece in both the migration puzzle (Kunz et al. 2008; Shamoun-Baranes et al., 2010a) and to general organismal biology (Schwenk et al. 2009). In terms of migration biology, this knowledge will help inform researchers about why animals migrate (e.g. climatic influence on availability of resources), how animals migrate (e.g. conserving energy through atmospheric assistance from wind, currents, or thermal convection), how migration affects fitness (e.g. the survival consequences of animals' responses to environmental conditions), and how migration evolves (e.g. potential role of regional winds or leading lines in shaping migratory flyways).

Conservation of migratory species

Declines in a host of migratory species, from songbirds to salmon and whales to wildebeest, have led some conservation biologists to conclude that the world's great animal migrations are endangered phenomena (Fleming and Eby 2003; Wilcove 2008). While many of the species undertaking migrations may not be in immediate danger of extinction, severe population declines of migratory animals could lead to changes in the structure, health, and functioning of entire ecosystems (Kunz et al. 2008). Conserving these migrants poses major scientific and political challenges. Given how profoundly the act of migration shapes the life-history of animals, and given how little is known about so many aspects of migration, it is not too much of an exaggeration to suggest that almost any integrative research on migration could yield important insights for conservation. There are four areas, however, where additional research is almost certain to produce urgently needed information for the conservation of migratory animals.

Basic life history information

It is impossible to protect a migratory animal without knowing where it goes, yet our knowledge of the pathways and destinations of most migrants is fragmentary at best and almost non-existent at worse. Fortunately, recent advances in telemetry and tracking have revolutionized this aspect of research. For example, Croxall et al. (2005) used satellite transmitters to study the movements of gray-headed albatrosses across the southern oceans; they discovered that individuals within a breeding population employed one of three distinct strategies. Birds using a given strategy followed consistent migratory routes and used the same staging areas. Such basic information is vital for reducing mortality related to fisheries operations, which is now the primary threat to albatrosses and many other seabirds. Options for tracking smaller animals are limited (Wikelski et al. 2007), but ~1 g light-sensitive loggers were recently used to track ~40 g migrants (Stutchbury et al. 2009), and stable isotopes have been used for many years to estimate where migratory animals molt or shed (reviewed in Hobson and Wassenaar 2008).

Understanding seasonal interactions

From a conservation perspective, understanding seasonal interactions allows us to predict how events at any one stage of the life cycle, or the combined events of all stages, will influence the population dynamics of migrants. For example, illegal logging in the central Mexican forests where almost all of the monarch butterflies of eastern North America winter is thought to reduce the thermal protection provided by the trees and to expose the diapausing insects to greater mortality due to cold, inclement weather. Winter storms in 1991–92, 1995–96, 2001–02, and 2003–04 resulted in the deaths of millions of monarchs, yet butterfly-watchers did not report any long-term population declines in the number of monarchs on the breeding grounds (with the important caveat that the monitoring of butterfly populations is fragmentary in North America). This begs the question of how much winter mortality (and loss of winter habitat) the monarchs can sustain before the population declines sharply. There has been a puzzling drop in the proportion of female butterflies on the wintering grounds over the past 30 years (Davis and Rendon-Salinas 2010), but here too we do not know how this shift in the sex ratio may affect populations over the long term because we do not understand seasonal interactions in this species.

Synchronicity, phenology, and climatic change

Many animal migrations are tied to phenological events. For example, red knots, semipalmated sandpipers (*Calidris pusilla*), ruddy turnstones (*Arenaria interpres*), and other shorebirds time their spring stopover in Delaware Bay to overlap the inshore migration of horseshoe crabs (*Limulus polyphemus*). Horseshoe crabs spawn in shallow water, and their eggs are an important food for the birds.

In fact, a 75% decline in the population of red knots migrating through the area has been linked, at least in part, to the overharvest of horseshoe crabs in the 1990's (Niles et al. 2009). The migration of wildebeest and zebras in the Serengeti is tied to the seasonal rains that generate new forage. How these, and other, migrations will fare in the wake of global climatic change is of growing concern to conservationists. In a landmark study, Both et al. (2006) attributed declines in populations of pied flycatchers (*Ficedula hypoleuca*) in the Netherlands to a disruption of the synchronicity between the flycatchers' migration and the emergence of caterpillars caused by climatic change. These flycatchers require an abundant supply of caterpillars to feed their offspring; the caterpillars appear after the emergence of leaves. In apparent response to rising temperatures in the Netherlands, leaves and therefore caterpillars are emerging earlier in the spring. The flycatchers, however, have not adjusted the timing of their arrival to the Netherlands, perhaps because they use a stable cue, such as photoperiod, on their African wintering grounds to trigger their northward migration. Thus, the peak of the caterpillar emergence no longer corresponds to the time when the birds are feeding their young. A similar, climate-driven disruption of the timing of caterpillar emergence and bird migration may threaten migratory songbirds in North America (Strode 2003).

Organisms that use the aerosphere are also influenced by an increasing number of anthropogenic factors, such as communication towers and wind turbines, that now dot the Earth's landscape (Desholm et al. 2006; Kunz et al. 2007a, 2007b; NRC 2007; Arnett et al. 2008; WWEA 2009). Human alteration of landscapes is rapidly and irreversibly transforming the quantity and quality of available habitats that airborne organisms rely upon for navigational cues, for sources of food, water, and for use as nesting and roosting habitats—conditions that in turn are influencing the structure and function of terrestrial and aquatic ecosystems and the assemblages of organisms therein. Climatic change and its expected increase in global temperatures, altered circulation of air masses, and its effects on local, regional, and weather patterns have had, and will continue to exert, profound influences on the dispersal, foraging and migratory behavior of arthropods, birds, and bats (Bowlin and Wikelski 2008; Kunz et al. 2008). Understanding how climatic change will affect animal migrations will therefore require integrated research across a range of disciplines.

Flexibility and adaptability

The degree to which changes to the migratory landscape will affect animals depends in large part on the ability of the animals in question to alter the timing, direction, and destinations of their journeys. Migration in birds has both endogenous and exogenous control mechanisms. As a result, birds have demonstrated the ability to alter migratory behaviors over remarkably short periods of time. House finches (*Carpodacus mexicanus*) from an allegedly non-migratory population in southern California were released in Long Island, New York in the early 1940s and quickly established an expanding population in the northeastern US. Within several decades, 28–54% of the house finches in the Northeast were migrating back and forth in southerly and northerly direction in excess of 50 km (Able and Belthoff 1998). A sizeable fraction of the blackcaps (*Sylvia atricapilla*) in central Europe, which used to migrate almost exclusively to Mediterranean and African wintering grounds, have altered their route over the past 40 years and now winter in the British Isles, where a combination of warmer temperatures and bird feeders boosts survival (Berthold 2001; Bearhop et al. 2005). Migratory populations may also adjust to long-term anthropogenic changes by altering morphological traits, as has recently been shown in a group of Neotropical migrants (Desrochers 2010). That animals can alter aspects of their migrations is clear; what is less clear is which species are able to do so and to what extent and how quickly. Understanding these limits, which will be critical for the effective conservation of some species, will require a detailed understanding of the mechanisms underlying the development of migratory behaviors, particularly the physiological and ecomechanical ones (Denny and Helmuth 2009). In the long term, integrated research that is itself incorporated into policy making will be crucial for preserving many of the world's animal migrations.

The future of migration biology

The phenomenon of migration presents a unique opportunity to address some of the grand challenges in organismal biology, but integrative research on migration has also greatly advanced our understanding of migration and will continue to do so. Within the next decade, we anticipate that technological and methodological advances such as light loggers (Stutchbury et al. 2009), global satellite tracking systems for small animals (Wikelski et al. 2007), and atmospheric simulations (Pielke et al. 1992; Walko et al. 2000; Cotton et al. 2003) will make it possible to directly address some important questions. For example, technologies that allow us to track migrants year-round (Wikelski et al. 2007; Robinson et al. 2010), coupled with research on individual reproductive success and survival, can help us to understand not only how populations are regulated (Runge and Marra 2005; Wilcove and Wikelski 2008) and the importance of currencies such as energy and time during migration, but also how migration itself evolves (Robinson et al. 2010).

The other challenges in animal migration will follow, but only if we continue to implement interdisciplinary research. For example, we need geneticists to explore the genes that are expressed in rapidly refueling migratory birds, hydrologists to help understand the effects of ocean currents on migrating whales, and evolutionary biologists to examine the historical factors that have led caribou to migrate, before we can say how, where, when and why animals migrate. Studying the effects of migrants on their environments and vice-versa also requires an interdisciplinary approach; aeroecology and migratory disease ecology, for example, cannot advance without atmospheric scientists and microbial biologists. Integrative research is needed because migration is an extremely complex phenomenon. Luckily, such research is becoming more common as collaboration becomes the rule rather than the exception and an increasing number of graduate students and post-doctoral researchers receive training in multiple disciplines. If migration researchers continue to adopt and facilitate integrative research programs, we may soon have to brainstorm a new set of grand challenges for migration biology.

Funding

SICB's Divisions of Animal Behavior, Neurobiology, and Comparative Endocrinology all donated money to support the symposium, and MIGRATE (an NSF-funded Research Coordination Network) donated money to cover NS's travel expenses. M.W., M.S.B., and I.-A.B. also received an NSF grant to fund the symposium (IOS proposal #0950470).

Acknowledgments

This article is based on a talk given by M.S.B. and I.-A.B. in the Integrative Migration Biology symposium at the 2010 Society for Integrative and Comparative Biology meeting in Seattle, Washington. The idea to hold the symposium originated in a MIGRATE workshop.

References

Able KP. 1982. Skylight polarization patterns at dusk influence migratory orientation in birds. Nature 299:550–51.

Able KP, Belthoff JR. 1998. Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America. Proc R Soc B 1410:2063–71.

Åkesson S, Alerstam T, Hedenström A. 1996a. Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. J Avian Biol 27:95–102.

Åkesson S, Hedenström A. 2000. Selective flight departure in passerine nocturnal migrants. Behav Ecol Sociobiol 47:140–44.

Åkesson S, Hedenström A. 2007. How migrants get there: migratory performance and orientation. BioScience 57:123–33.

Åkesson S, Karlsson L, Pettersson J, Walinder G. 1992. Body contents and migration strategies: a comparison between Robins *Erithacus rubecula* from two stop-over sites in Sweden. Vogelwarte 36:188–95.

Åkesson S, Karlsson L, Walinder G, Alerstam T. 1996b. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in South Scandinavia. Behav Ecol Sociobiol 38:293–302.

Åkesson S, Walinder G, Karlsson L, Ehnbom S. 2002. Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. J Avian Biol 33:349–57.

Åkesson S. 1993. Coastal migration and wind compensation in nocturnal passerine migrants. Ornis Scand 24:87–94.

Åkesson S. 1994. Comparative orientation experiments with different species of long-distance migrants: effect of magnetic field manipulation. Anim Behav 48:1379–93.

Åkesson S. 1999. Do passerines captured at an inland ringing site perform reverse migration in autumn? ARDEA 87:129–38.

Alerstam T, Hedenström A, Åkesson S. 2003. Long-distance migration: evolution and determinants. Oikos 103:247–60.

Alerstam T, Hedenström A. 1998. The development of bird migration theory. J Avian Biol 29:343–69.

Alpert P, Niyogi D, Pielke RA, Eastman JL, Xue YK, Raman S. 2006. Evidence for carbon dioxide and moisture interactions from the leaf cell up to global scales: perspective on human-caused climate change. Glob Planet Change 54:202–8.

Arnett EB, et al. 2008. Patterns of bat fatalities at wind energy facilities in North America. J Wildl Manage 72:61–78.

Baker AJ, Gonzalez PM, Piersma T, Niles LJ, do Nascimento IDS, Atkinson PW, Clark NA, Minton CDT, Peck MK, Aarts G. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proc Roy Soc B 271:875–82.

Barta Z, McNamara JM, Houston AI, Weber TP, Hedenström A, Feró O. 2008. Optimal moult strategies in migratory birds. Phil Trans R Soc B 363:211–29.

Bauer S, van Dinther M, Høgda K-A, Klaassen M, Madsen J. 2008. The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. J Anim Ecol 77:654–60.

Bearhop S, Hilton GM, Votier SC, Waldron S. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. Proc R Soc B 271(Suppl):S215–8.

Bearhop S, Fiedler W, Furness RW, Votier SC, Waldron S, Newton J, Bowen GJ, Berthold P, Farnsworth K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. Science 310:502–4.

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

Bensch S, Grahn M, Muller N, Gay L, Åkesson S. 2009. Genetic, morphological, and feather isotope variation of migratory willow warblers show gradual divergence in a ring. Mol Ecol 18:3087–96.

Berthold P. 2001. Bird migration: a general survey. Oxford: Oxford University Press.

Berthold P. 2003. Genetic basis and evolutionary aspects of bird migration. Adv Study Behav 33:175–229.

Bêty J, Giroux J-F, Gauthier G. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behav Ecol Sociobiol 57:1–8.

Bisson I-A, Marra PP, Burtt EH, Sikaroodi M, Gillevet PM. 2007. A molecular comparison of plumage and soil bacteria across biogeographic, ecological, and taxonomic scales. Microb Ecol 54:65–81.

Bisson I-A, Safi K, Holland RA. 2009a. Evidence for repeated independent evolution of migration in the largest family of bats. PloS One 4:e7504.

Bisson I-A, Marra PP, Burtt EH, Sikaroodi M, Gillevet PM. 2009b. Variation in plumage microbiota depends on season and migration. Microb Ecol 58:212–20.

Bonner JT, Koontz PG Jr, Paton D. 1953. Size in relation to the rate of migration in the slime mold *Dictyostelium discoideum*. Mycol 45:235–40.

Both C, Bouwhuis S, Lessells CM, Visser ME. 2006. Climate change and population declines in a long-distance migratory bird. Nature 441:81–3.

Bowlin MS, Wikelski M. 2008. Pointed wings, low wingloading and calm air reduce migratory flight costs in songbirds. PLoS One 3:e2154.

Bryant DM. 1983. Heat stress in tropical birds: behavioural thermoregulation during flight. Ibis 125:313–23.

Burtt EH Jr, Ichida JM. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. Auk 116:364–72.

Butler PJ, Woakes AJ, Bishop CM. 1998. Behaviour and physiology of Svalbard barnacle geese, *Branta leucopsis*, during their autumn migration. J Avian Biol 29:536–45.

Calisher CH, Childs JE, Field HE, Holmes KV, Schountz T. 2006. Bats: important reservoir hosts of emerging viruses. Clin Microbiol Rev 19:531–45.

Cerasale DJ, Guglielmo CG. 2006. Dietary effects on prediction of body mass changes in birds by plasma metabolites. Auk 123:836–46.

Chapman JW, Nesbit RL, Burgin LE, Reynolds DR, Smith AD, Middleton DR, Hill JK. 2010. Flight orientation behaviors promote optimal migration trajectories in high-flying insects. Science 327:682.

Cochran WW, Mouritsen H, Wikelski M. 2004. Migrating songbirds recalibrate their magnetic compass daily from twilight cues. Science 304:405–8.

Cochran WW, Wikelski M. 2005. Individual migratory tactics of New World *Catharus* thrushes. In: Greenberg R, Marra PP, editors. Birds of two worlds: the ecology and evolution of temperate-tropical migration systems. Baltimore, MD: Johns Hopkins University Press. p. 274–89.

Cochran WW, Bowlin MS, Wikelski M. 2008. Wingbeat frequency and flap-pause ratio during natural flight in thrushes. Integr Comp Biol 48:134–51.

Cotton WR, et al. 2003. RAMS 2001: current status and future directions. Meteorol Atmos Phys 82:5–29.

Couzin ID, Krause J, Franks NR, Levin SA. 2005. Effective leadership and decision-making in animal groups on the move. Nature 433:513–6.

Croxall JP, Silk JRD, Phillips RA, Afanasyev V, Briggs DR. 2005. Global circumnavigations: Tracking year-round ranges of nonbreeding albatrosses. Science 307:249–50.

Cryan PM, Diehl RH. 2009. Analyzing bat migration. In: Kunz TH, Parsons S, editors. Ecological and behavioral methods for the study of bats. Baltimore: Johns Hopkins University Press. p. 476–89.

Dänhardt J, Lindström A. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Anim Behav 62:235–43.

Davis AK, Rendon-Salinas E. 2010. Are female monarch butterflies declining in eastern North America? Evidence of a 30-year change in sex ratios at Mexican overwintering sites. Biol Lett 6:45–7.

Denny M, Helmuth B. 2009. Confronting the physiological bottleneck: a challenge from ecomechanics. Integr Comp Biol 49:197–201.

Denver JR, Hopkins PM, McCormick SD, Propper CR, Riddiford L, Sower SA, Wingfield JC. 2009. Comparative endocrinology in the 21st century. Integr Comp Biol 49:339–48.

Desholm M, Fox AD, Beasley PDL, Kahlert J. 2006. Remote techniques for counting and estimating the number of bird-wind turbine collisions at sea: a review. Ibis 148:76–89.

Desrochers A. 2010. Morphological response of songbirds to 100 years of landscape change in North America. Ecology. In press.

Dick WJA, Piersma T, Prokosch P. 1987. Spring migration of the Siberian knots *Calidris canutus canutus*: results of a co-operative Wader Study Group project. Ornis Scand 18:5–16.

Dietz MW, Piersma T. 2007. Red knots give up flight capacity and defend food processing capacity during winter starvation. Funct Ecol 21:899–904.

Dietz MW, Piersma T, Hedenström A, Brugge M. 2007. Intraspecific variation in avian pectoral muscle mass: constraints on maintaining manoeuvrability with increasing body mass. Funct Ecol 21:317–26.

Dingle H. 1996. Migration: the biology of life on the move. New York: Oxford University Press.

Dingle H, Drake VA. 2007. What is migration? Bioscience 57:113–21.

Drake VA, Farrow RA. 1988. The influence of atmospheric structure and motions on insect migration. Ann Rev Entomol 33:183–210.

Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. PNAS: published online (doi/10.1073/pnas.0909493107).

Emlen ST. 1975. The stellar orientation system of a migratory bird. Sci Am 233:102–11.

Erni B, Liechti F, Bruderer B. 2005. The role of wind in passerine autumn migration between Europe and Africa. Behav Ecol 16:732–40.

Fleming TH. 1995. The use of stable isotopes to study the diets of plant-visiting bats. Sym Zool S 67: 99–110.

Fleming TH, Eby P. 2003. Ecology of bat migration. In: Kunz TH, editor. Bat ecology. Chicago: The University of Chicago Press. p. 156–208.

Fleming TH, Nuñez RA, Sternberg L. 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. Oecologia 94:72–5.

Frederiksen M, Lebreton J-D, Bregnballe T. 2001. The interplay between culling and density-dependence in the great cormorant: a modeling approach. J Appl Ecol 38:617–27.

Fuller MR, Millspaugh JJ, Church KK, Kenward RE. 2005. Wildlife radiotelemetry. In: Bookhout TA, editor. Research and management techniques for wildlife and habitats. Bethesda, MD: The Wildlife Society. p. 377–417.

Gannes LZ. 2001. Comparative fuel use of migrating passerines: effects of fat stores, migration distance, and diet. Auk 118:665–77.

Gargas A, Trest MT, Christiensen M, Volk TJ, Blehert DS. 2009. *Geomyces destructans* sp. nov. associated with bat white-nose syndrome. Mycotoxon 108:147–54.

Gaspar P, Georges JY, Fossette S, Lenoble A, Ferraroli S, Le Maho Y. 2006. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. Proc R Soc B 273:2697–702.

Gauthier G, Pradel R, Menu S, Lebreton J-D. 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. Ecology 82:3105–19.

Gibo DL, Pallett MJ. 1979. Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera, Danaidae), during the late summer migration in southern Ontario. Can J Zool 57:1393–401.

Gibo DL. 1981. Some observations on soaring flight in the mourning cloak butterfly (*Nymphalis antiopa* L.) in southern Ontario. J NY Entomol Soc 89:98–101.

Gill JA, Sutherland JW, Norris K. 2001. Depletion models can predict shorebird distribution at different spatial scales. Proc R Soc B 268:369–76.

Gill RE, Piersma T, Hufford G, Servranckx R, Riegen A. 2005. Crossing the ultimate ecological barrier: evidence for an 11000-km-long nonstop flight from Alaska to New Zealand and eastern Australia by bar-tailed godwits. Condor 107:1–20.

Gill RE, Tibbitts TL, Douglas DC, Handel CM, Mulcahy DM, Gottschalck JC, Warnock N, McCaffery BJ, Battley PF, Piersma T. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proc Roy Soc B 276:447–58.

Gonzalez-Solis J, Croxall JP, Oro D, Ramos R, Ruiz X. 2005. Migration strategies in relation to the population of origin: the case of Cory's shearwaters tracked by GLS. Alauda 73:221.

Goss-Custard JD, et al. 1995a. Population consequences of winter habitat loss in a migratory shorebird. I. Estimating model parameters. J Anim Ecol 32:320–36.

Goss-Custard JD, Clarke RT, le V dit Durell SEA, Caldow RWG, Ens BJ. 1995b. Population consequences of winter habitat loss in a migratory shorebird. II. Model predictions. J Anim Ecol 32:320–36.

Gresh T, Lichatowich J, Schoonmaker P. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25:15–21.

Grodzinkski U, Spegel O, Korine C, Holderied MW. 2009. Context-dependent flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus kuhlii*. J Anim Ecol 78:540–48.

Guglielmo CG, Cerasale DJ, Eldermire C. 2005. A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiol Biochem Zool 78:116–25.

Guglielmo CG, Piersma T, Williams TD. 2001. A sport physiological perspective on bird migration: evidence for flight-induced muscle damage. J Exp Biol 201:2683–90.

Gylfe A, Bergström S, Lundström J, Olsen B. 2000. Reactivation of Borrelia infection in birds. Nature 403:724–5.

Gwinner E. 1973. Circannual rhythms in birds: their interaction with circadian rhythms and environmental photoperiod. J Reprod Fertil Suppl 19:51–65.

Hahn TP, MacDougall-Shackleton SA. 2007. Adaptive specialization, conditional plasticity and phylogenetic history in the reproductive cue response system of birds. Phil Trans R Soc B 363:267–86.

Hasselquist D, Lindström Å, Jenni-Eiermann S, Koolhaas A, Piersma T. 2007. Long flights do not influence immune responses of a long-distance migrant bird: a wind-tunnel experiment. J Exp Biol 210:1123–31.

Hedenström A. 2003. Scaling migration speed in animals that run, swim and fly. J Zool 259:155–60.

Hedenström A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Phil Trans R Soc B 363:287–99.

Hedenström A, Alerstam T. 1996. Skylark optimal flight speeds for flying nowhere and somewhere. Behav Ecol 7:121–6.

Hedenström A, Alerstam T. 1995. Optimal flight speed of birds. Phil Trans R Soc B 348: 471–87.

Hedenström A, Alerstam T. 1998. How fast can birds migrate? J Avian Biol 29:424–32.

Heitmeyer ME, Fredrickson LH. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence mallard recruitment? T N Am Wildl Nat Res 46:44–57.

Hobson KA. 2007. Isotopic tracking of migratory wildlife. In: Michener RH, Lajtha K, editors. Stable isotopes in ecology and environmental science. Malden: Blackwell Publishing. p. 155–75.

Hobson KA, Wassenaar LI. 2008. Tracking animal migration with stable isotopes. Volume 2, Terrestrial Ecology Series. San Diego: Academic Press.

Holland RA, Wikelski M, Wilcove DS. 2006a. How and why do insects migrate? Science 313:794–6.

Holland RA, Thorup K, Vonhof MJ, Cochran W, Wikelski M. 2006b. Bat orientation using Earth's magnetic field. Nature 444:702.

Holland RA, Wikelski M. 2009. Studying the migratory behavior of individual bats: current techniques and future directions. J Mammal 90:1324–29.

Holland RA, Wikelski M, Kummeth F, Bosque C. 2009. The secret life of oilbirds: new insights into the movement ecology of a unique avian frugivore. PLoS ONE 4:e8264.

Horvitz N. 2009. Slow and safe or fast and risky: a comparative analysis of soaring-gliding flight performance. M.Sc. Thesis. Israel: The Hebrew University of Jerusalem.

Hubalék Z. 2004. An annotated checklist of pathogenic microorganisms associated with migratory birds. J Wildlife Dis 40:639–59.

Jenni-Eiermann S, Jenni L. 1994. Plasma metabolite levels predict individual body-mass changes in a small long-distance migrant, the garden warbler. Auk 111:888–99.

Kalnay E, et al. 1996. The NCEP/NCAR 40-year reanalysis project. Bull Amer Meteorol Soc 77:437–71.

Kaminski RM, Gluesing EA. 1987. Density- and habitat related recruitment in mallards. J Wildlife Manage 51:141–8.

Karasov WH, Pinshow B. 2000. Test for physiological limitation to nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. Physiol Biochem Zool 73:335–43.

Killingley JS. 1980. Migrations of California gray whales by oxygen-18 variations in their epizoic barnacles. Science 207:759–60.

Klaasen RHG, Strandberg R, Hake M, Alerstam T. 2008. Flexibility in daily travel routines causes regional variation in bird migration speed. Behav Ecol Sociobiol 62:1427–32.

Klaassen M, Bauer S, Madsen J, Tombre I. 2006. Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. J Appl Ecol 43:92–100.

Klaassen M, Biebach H. 1994. Energetics of fattening and starvation in the long distance migratory garden warbler, *Sylvia borin*, during the migratory phase. J Comp Physiol B 164:362–71.

Kunz TH, Arnett EB, Cooper BM, Erickson WP, Hoar AR, Larkin RP, Mabee T, Morrison ML, Strickland MD, Szewczak JM. 2007a. Assessing impacts of wind energy development on nocturnally active birds and bats: a guidance document. J Wildl Manage 71:2449–86.

Kunz TH, Arnett EB, Erickson WP, Johnson GD, Larkin RP, Strickland MD, Thresher RW, Tuttle MD. 2007b. Ecological impacts of wind energy development on bats: questions, hypotheses, and research needs. Front Ecol Environ 5:315–24.

Kunz TH, et al. 2008. Aeroecology: probing and modeling the aerosphere. Integr Comp Biol 48:1–11.

Kunz TH, Wrazen JA, Burnett CD. 1998. Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*). Ecoscience 5:8–17.

Kvist A, Lindstrom A, Green M, Piersma T, Visser GH. 2001. Carrying large fuel loads during sustained bird flight is cheaper than expected. Nature 413:730–32.

Landys M, Ramenofsky M, Wingfield JC. 2006. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. Gen Comp Endocrinol 148:132–49.

Lau SKP, Woo PCY, Li KSM, Huang Y, Tsoi H-W, Wong BHL, Wong SSY, Leung S-Y, Chan K-H, Yuen K-Y. 2005. Severe acute respiratory syndrome coronavirus-like virus in Chinese horseshoe bats. PNAS 102:14040–5.

Lawton JH, May RM. 1983. The birds of Selbourne. Nature 306:732–3.

Lebreton J-D. 2005. Dynamical and statistical models for exploited populations. Aust Nz J Stat 47: 49–63.

Leshem Y, Yom-Tov Y. 1996. The use of thermals by soaring migrants. Ibis 138:667–74.

Leyrer J, Bocher P, Robin F, Delaporte P, Goulevent C, Joyeux E, Meunier F, Piersma T. 2009. Northward migration of Afro-Siberian knots *Calidris canutus canutus*: high variability in red knots numbers visiting stopover sites on French Atlantic coast (1979-2009). Wader Study Group Bull 116:145–51.

Li W, et al. 2005. Bats are natural reservoirs of SARS-like coronaviruses. Science 310:676–9.

Liechti F. 2006. Birds: blowin' by the wind? J Ornithol 147:202–11.

Lindström Å, Alerstam T. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. Am Nat 140: 477–91.

Lindström Å. 1991. Maximum fat deposition rates in migrating birds. Ornis Scand 22:12–9.

Lindström Å, Kvist A, Piersma T, Dekinga A, Dietz MW. 2000. Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. J Exp Biol 203:913–9.

Liu J, et al. 2005. Highly pathogenic H5N 1 influenza virus infection in migratory birds. Science 309:1206.

Lucas FS, Broennimann O, Febbraro I, Heeb P. 2003. High diversity among feather-degrading bacteria from a dry meadow soil. Microb Ecol 45: 282–90.

Luschi P, Hays GC, Papi F. 2003. A review of long-distance movements by marine turtles, and the possible role of ocean currents. Oikos 103:293–302.

Madigan MT, Martinko JM, Parker J. 1996. Brock biology of microorganisms. Upper Saddle River. NJ: Prentice-Hall.

Mandel JT, Bildstein KL, Bohrer G, Winkler DW. 2008. Movement ecology of migration in turkey vultures. PNAS 105:19102–7.

Marra PP, Hobson KA, Holmes RT. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–6.

Marra PP, Griffing S, Cafree CL, Kilpatrick AM, Mclean R, Brand C, Kramer L, Novak R. 2004. West Nile virus and wildlife. Bioscience 54:393–402.

Marra PP, Norris DR, Haig SM, Webster M, Royle A. 2006. Migratory connectivity. In: Crooks K, Muttulingam S, editors. Maintaining connections for nature. Oxford: Oxford University Press. p. 157–83.

Marra PP, Studds CE. 2010. Migratory connectivity. In: Breed MD, Moore J, editors. Encyclopedia of Animal Behavior. Elsevier Science, Oxford: Academic Press.

McGuire LP, Fenton MB, Faure PA, Guglielmo CG. 2009. Determining feeding state and rate of mass change in insectivorous bats using plasma metabolite analysis. Physiol Biochem Zool 82:812–8.

McNamara JM, Houston AI. 2008. Optimal annual routines: Behaviour in the context of physiology and ecology. Phil Trans R Soc B 363:301–19.

McNamara JM, Welham RK, Houston AI. 1998. The timing of migration within the context of an annual routine. J Avian Biol 29:416–23.

McWilliams SR, Karasov WH. 2001. Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance. Comp Biochem Physiol 128A:579–93.

Mihelsons HA, Mednis AA, Blums PB. 1985. Regulatory mechanisms of numbers in breeding populations of migratory ducks. Proc Int Ornithol Congr Moscow 18:797–802.

Muheim R, Moore FR, Phillips JB. 2006a. Calibration of magnetic and celestial compass cues in migratory birds – a review of cue-conflict experiments. J Exp Biol 209:2–17.

Muheim R, Phillips JB, Åkesson S. 2006b. Polarized light cues underlie compass calibration in migratory songbirds. Science 313:837–9.

Muheim R, Åkesson S, Phillips JB. 2007. Magnetic compass of migratory savannah sparrows is calibrated by skylight polarization at sunrise and sunset. J Ornithol 148 (Suppl 2):485–94.

Muheim R, Phillips JB, Deutschlander ME. 2009. White-throated sparrows calibrate their magnetic compass by polarized light cues during both autumn and spring migration. J Exp Biol 212:3466–72.

Muhkin A, Kosarev V, Ktitorov P. 2005. Nocturnal life of young songbirds well before migration. Proc R Soc B 272:1535–9.

Nathan R, et al. 2005. Long-distance biological transport processes through the air: Can nature's complexity be unfolded in-silico? Div Distr 11:131–7.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008. A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci USA 105:19052–9.

Nee S. 2004. More than meets the eye. Nature 429:804–5.

Newton I. 2004. Population limitation in migrants. Ibis 146:197–226.

Newton I. 2008. The migration ecology of birds. New York: Elsevier.

Niles LJ, et al. 2009. Effects of horseshoe crab harvest in Delaware Bay on red knots: are harvest restrictions working? BioScience 59:153–64.

Norberg UM. 1990. Vertebrate flight. Berlin: Springer.

Norberg UM, Rayner JMV. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): Wing adaptations, flight performance, foraging strategy, echolocation. Phil Trans R Soc B 316:335–427.

Norris DR. 2005. Carry-over effects and habitat quality in migratory populations. Oikos 109:178–86.

NRC (National Research Council) 2007. Environmental Impacts of Wind-Energy Projects. Washington, DC: The National Academies Press.

Olff H, Alonso D, Berg MP, Eriksson BK, Loreau M, Piersma T, Rooney N. 2009. Parallel ecological networks in ecosystems. Phil Trans R Soc B 364:1755–79.

Olsen B, Munster VJ, Wallensten A, Waldenström J, Osterhaus ADME, Fouchier RAM. 2006. Global patterns of influenza A virus in wild birds. Science 312:384–8.

Pennycuick CJ. 1972. Soaring behavior and performance of some East African birds observed from a motorglider. Ibis 114:178–218.

Pennycuick CJ. 1998. Towards an optimal strategy for bird flight research. J Avian Biol 29:449–57.

Pennycuick CJ. 2008. Modeling the Flying Bird. Boston: Academic Press/Elsevier.

Pettifor RA, Caldow RWG, Rowcliffe JM, Goss-Custard JD, Black JM, Hodder KH, Houston AI, Lang A, Webb J. 2000. Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. J. Appl. Ecol. 37:103–35.

Pielke RA, et al. 1992. A comprehensive meteorological modeling system — RAMS. Meteorol Atmos Phys 49:69–91.

Pierce BJ, McWilliams SR, O'Connor TP, Place AR, Guglielmo CG. 2005. Effect of dietary fatty acid composition on depot fat and exercise performance in a migrating songbird, the red-eyed vireo. J Exp Biol 208:1277–85.

Piersma T, Gudmundsson GA, Lilliendahl K. 1999. Rapid changes in the size of different functional organ and muscle groups during refuelling in a long-distance migrant shorebird. Physiol Biochem Zool 72:405–15.

Piersma T, Rogers DI, González PM, Zwarts L, Niles LJ, de Lima S, do Nascimento I, Minton CDT, Baker AJ. 2005. Fuel storage rates before northward flights in red knots worldwide: facing the severest ecological constraint in tropical intertidal environments? In: Greenberg R, Marra PP, editors. Birds of two worlds: the ecology and evolution of temperate-tropical migration systems. Baltimore: Johns Hopkins University Press. p. 262–73.

Polovina JJ, Balazs GH, Howell EA, Parker DM, Seki MP, Dutton PH. 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. Fish Oceanogr 13:36–51.

Price ER, Guglielmo CG. 2009. The effect of muscle phospholipid fatty acid composition on exercise performance: a direct test in the migratory white-throated sparrow (*Zonotrichia albicollis*). Am J Physiol Regul Integr Comp Physiol 297:R775–82.

Ramenofsky M, Wingfield JC. 2006. Behavioral and physiological conflicts in migrants: the transition between migration and breeding. J Ornithol 147:135–45.

Ramenofsky M, Moffat J, Bentley GE. 2008. Corticosterone and migratory behaviour of captive white-crowned sparrows. International proceedings of ICA-CPB, Pressures of Life: Molecules to Migration. Masai, Mara Game Reserve: Kenya. pp. 575–82.

Reed KD, Meece JK, Henkel JS, Shukla KS. 2003. Birds, migration and emerging zoonoses: West Nile virus, Lyme disease, influenza A and enteropathogens. Clin Med Res 1:5–12.

Reichard JD, Prajapati SI, Austad SN, Keller C, Kunz TH. 2010. Thermal windows on Brazilian free-tailed bats facilitate thermoregulation during prolonged flight. Proceedings of the 2010 Annual Society for Integrative and Comparative Biology Meeting. Seattle, Washington.

Reudink MW, Marra PP, Kyser TK, Boag PT, Langin KM, Ratcliffe L. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. Proc R Soc B 276:1619–26.

Reynolds AM, Reynolds DR, Riley JR. 2009. Does a 'turbophoretic' effect account for layer concentrations of insects migrating in the stable night-time atmosphere? J Roy Soc Interface 6:87–95.

Reynolds AM, Reynolds DR. 2009. Aphid aerial density profiles are consistent with turbulent advection amplifying flight behaviours: abandoning the epithet 'passive'. Proc R Soc B 276:137–43.

Richard H, Ivailo B, Björn S. 2010. A nocturnal mammal, the greater mouse-eared bat, calibrates a magnetic compass by the sun. Proceedings of the National Academy of Sciences (PNAS), published online (doi/10.1073/pnas.0912477107).

Richardson WJ. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–72.

Richardson WJ. 1990. Timing and amount of bird migration in relation to weather: updated review. In: Gwinner E, editor. Bird migration: physiology and ecophysiology. Berlin, Heidelberg: Springer. p. 78–101.

Robinson WD, Bowlin MS, Bisson I, Shamoun-Baranes J, Thorup K, Diehl RH, Kunz TH, Mabey S, Winkler DW. 2010. Integrating concepts and technologies to advance the study of bird migration. Front Ecol Environ: published online (doi:10.1890/080179).

Runge M, Marra PP. 2005. Modeling seasonal interactions in the annual cycle of migratory birds. In: Greenberg R, Marra PP, editors. Birds of two worlds: the ecology and evolution of temperate-tropical migration systems. Baltimore, MD: Johns Hopkins University Press. p. 375–89.

Saino N, Szép T, Ambrosini R, Romano M, Møller AP. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. Proc R Soc B 271:681–6.

Sandberg R. 2003. Stored fat and migratory orientation of birds. In: Berthold P, Gwinner E, Sonnenschein E, editors. Avian migration. Berlin, Heidelberg, New York: Springer. p. 515–25.

Sapir N. 2009. The effects of weather on bee-eater (*Merops apiaster*) migration. PhD Thesis. Israel: The Hebrew University of Jerusalem.

Satterlie RA, Pearse JS, Sebens KP. 2009. The black box, the creature from the Black Lagoon, August Krogh, and the dominant animal. Integr Comp Biol 49:89–92.

Sauer F. 1957. Die Sternenorientierung nächtlich ziehender Grasmücken (*Sylvia atricapilla, borin* und *currura*). Z Tierpsychol 14:20–70.

Schmidt-Nielsen K. 1972. Locomotion – energy cost of swimming, flying and running. Science 177:222–28.

Schwenk K, Padilla DK, Bakken GS, Full RJ. 2009. Grand challenges in organismal biology. Integr Comp Biol 49:7–14.

Schwilch R, Piersma T, Holmgren NMA, Jenni L. 2002. Do migratory birds need a nap after a long non-stop flight? Ardea 90:149–54.

Shamoun-Baranes J, Leshem Y, Yom-Tov Y, Liechti O. 2003a. Differential use of thermal convection by soaring birds over central Israel. Condor 105:208–18.

Shamoun-Baranes J, Liechti O, Yom-Tov Y, Leshem Y. 2003b. Using a convection model to predict altitudes of white stork migration over central Israel. Bound-Lay Meteorol 107:673–81.

Shamoun-Baranes J, Baharad A, Alpert P, Berthold P, Yom-Tov Y, Dvir Y, Leshem Y. 2003c. The effect of wind, season and latitude on the migration speed of white storks *Ciconia ciconia*, along the eastern migration route. J Avian Biol 34:97–104.

Shamoun-Baranes J, van Loon E, Alon D, Alpert P, Yom-Tov Y, Leshem Y. 2006. Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? Glob Ecol Biogeog 15:541–52.

Shamoun-Baranes J, Bouten W, van Loon E. 2010a. Integrating meteorological conditions into migration research. Proceedings of the 2010 Annual Society for Integrative and Comparative Biology Meeting. Seattle, Washington.

Shamoun-Baranes J, Leyrer J, van Loon E, Bocher P, Robin F, Meunier F, Piersma T. 2010b. Stochastic atmospheric assistance and the use of emergency staging sites by migrants. Proc R Soc B: published online (doi: 10.1098/rspb.2009.2112).

Shannon HD, Young GS, Yates MA, Fuller MR, Seegar WS. 2002a. American white pelican soaring flight times and altitudes relative to changes in thermal depth and intensity. Condor 104:679–83.

Shannon HD, Young GS, Yates MA, Fuller MR, Seegar WS. 2002b. Measurements of thermal updraft intensity over complex terrain using American white pelicans and a simple boundary-layer forecast model. Bound-Lay Meteorol 104:167–99.

Sillett TS, Holmes RT, Sherry TW. 2000. Impacts of a global climate cycle on the population dynamics of a migratory songbird. Science 288:2040–2.

Smith RJ, Moore FR. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behav Ecol Sociobiol 57:231–9.

Srygley RB, Oliveira EG, Dudley R. 1996. Wind drift compensation, flyways, and conservation of diurnal, migrant neotropical lepidoptera. Proc R Soc B 263:1351–7.

Stefanescu C, Alarcon M, Vila AA. 2007. Migration of the painted lady butterfly, *Vanessa cardui*, to north-eastern Spain is aided by African wind currents. J Anim Ecol 76:888–98.

Stokke BG, Møller AP, Saether BE, Rheinwald G, Gutscher H. 2005. Weather in the breeding area and during migration affects the demography of a small long-distance passerine migrant. Auk 122:637–47.

Strandberg R, Klaassen RHG, Hake M, Alerstam T. 2009. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. Biol Lett: published online (doi:10.1098/rsbl.2009.0785).

Strode PK. 2003. Implications of climate change for North American wood warblers (Parulidae). Glob Change Biol 9:1137–44.

Studds C, Kyser K, Marra PP. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. PNAS 105:2929–33.

Stutchbury BJM, Tarof SA, Done T, Gow E, Kramer PM, Tautrin J, Fox JW, Afanasyev V. 2009. Tracking long-distance songbird migration by using geolocators. Science 323:896.

Sullivan JC, Buscetta KJ, Michener RH, Whitaker JO Jr, Finnerty JR, Kunz TH. 2006. Models developed from δ^{13}C and δ^{15}N of skin tissue indicate non-specific habitat use by the big brown bat (*Eptesicus fuscus*). Ecoscience 13:11–22.

Taylor LR. 1986. Synoptic dynamics, migration and the Rothamsted Insect Survey – Presidential Address to the British Ecological Society, December 1984. J Anim Ecol 55:1–38.

Thorup K, Alerstam T, Hake M, Kjellen N. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. Proc R Soc B 270:S8–S11.

Torre-Bueno JR. 1976. Temperature regulation and heat dissipation during flight in birds. J Exp Biol 65:471–82.

van Gils JA, Piersma T, Dekinga A, Battley PF. 2006. Modelling phenotypic flexibility: an optimality analysis of gizzard size in red knots *Calidris canutus*. Ardea 94:409–20.

Waldenström J, Broman T, Carlsson I, Hasselquist D, Achterberg RP, Wagenaar JA, Olsen B. 2002. Prevalence of *Campylobacter jejuni*, *Campylobacter lari*, and *Campylobacter coli* in different ecological guilds and taxa of migrant birds. Appl Environ Microb 68:5911–7.

Walko RL, Avissar R. 2008. The Ocean-Land-Atmosphere Model (OLAM). Part I: shallow-water tests. Mon Weather Rev 136:4033–44.

Walko RL, et al. 2000. Coupled atmosphere-biophysics-hydrology models for environmental modeling. J Appl Meteorol 39:931–44.

Weber J-M. 2009. The physiology of long-distance migration: extending the limits of endurance metabolism. J Exp Biol 212:593–7.

Webster MS, Marra PP. 2005. The importance of understanding migratory connectivity. In: Greenberg R, Marra PP, editors. Birds of two worlds: the ecology and evolution of temperate-tropical migration systems. Baltimore, MD: Johns Hopkins University. p. 199–209.

Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT. 2002. Links between worlds: unraveling migratory connectivity. TREE 17:76–83.

Wiersma P, Piersma T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy-expenditure in the annual cycle of red knots. Condor 96:257–79.

Wikelski M, Moskowitz D, Adelman JS, Cochran J, Wilcove DS, May ML. 2006. Simple rules guide dragonfly migration. Biol Lett 2:325–9.

Wikelski M, Kays RW, Kasdin J, Thorup K, Smith JA, Cochran WW, Swenson GW Jr. 2007. Going wild – what a global small-animal tracking system could do for experimental biologists. J Exp Biol 210:181–6.

Wilcove DS, Wikelski M. 2008. Going, going, gone: Is animal migration disappearing? PLOS Biol 6:1361–4.

Wilcove DS. 2008. No way home: the decline of the world's great animal migrations. Washington, DC: Island Press.

Williams CB. 1957. Insect migration. Ann Rev Entomol 2:163–80.

Wiltschko W, Wiltschko R. 1995. Magnetic orientation in animals. Berlin: Springer.

Wingfield JC. 2008. Organization of vertebrate annual cycles: implications for control mechanisms. Phil Trans R Soc 363:425–41.

WWEA 2009. World wind energy report 2008. World Wind Energy Association. (http://wwindea.org) [accessed January 12, 2010].

Zehnder S, Åkesson S, Liechti F, Bruderer B. 2002. Observations of free-flying nocturnal migrants at Falsterbo: occurrence of reverse flight directions in autumn. Avian Science 2:103–13.