9-1-2010

Integrating Concepts and Technologies to Advance the Study of Bird Migration

W. Douglas Robinson
Oregon State University, douglas.robinson@oregonstate.edu

Melissa Bowlin
Lund University

Isabelle Bisson
Princeton University

Judy Shamoun-Barnes
University of Amsterdam

Kasper Thorup
University of Copenhagen

See next page for additional authors

Authors
W. Douglas Robinson, Melissa Bowlin, Isabelle Bisson, Judy Shamoun-Barnes, Kasper Thorup, Robert H. Diehl, Thomas H. Kunz, Sarah Mabey, and David W. Winkler

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W Douglas Robinson[1*], Melissa S Bowlin[2], Isabelle Bisson[3], Judy Shamoun-Baranes[4], Kasper Thorup[5], Robert H Diehl[6], Thomas H Kunz[7], Sarah Mabey[8], and David W Winkler[9]

Recent technological innovation has opened new avenues in migration research – for instance, by allowing individual migratory animals to be followed over great distances and long periods of time, as well as by recording physiological information. Here, we focus on how technology – specifically applied to bird migration – has advanced our knowledge of migratory connectivity, and the behavior, demography, ecology, and physiology of migrants. Anticipating the invention of new and smaller tracking devices, in addition to the ways that technologies may be combined to measure and record the behavior of migratory animals, we also summarize major conceptual questions that can only be addressed once innovative, cutting-edge instrumentation becomes available.

Front Ecol Environ 2010; 8(7): 354–361, doi:10.1890/080179 (published online 21 Aug 2009)

Billions of organisms, ranging from bats to butterflies and whales to wildebeest, engage in repeated movements between seasonally favorable environments. These movements vary from distances of a few to thousands of kilometers. Many birds, for example, spend more than half of each year in equatorial regions, and then fly great distances to breed in temperate locations. Others move even farther, leaving their temperate northern breeding range as winter approaches and traveling to temperate habitats in the Southern Hemisphere, as spring arrives there. Yet, despite the enormous number of individuals involved in such migrations, there are large gaps in our understanding of many aspects of migration. Even basic information, such as locations where individual organisms choose to breed and overwinter, remains rare and elusive. Acquisition and integration of knowledge gained as a result of technological advances will improve our understanding of many of the basic mechanisms affecting the ecology and evolution of migratory animals (Webster *et al.* 2002). Although many taxa migrate, we focus here on birds, for two reasons. First, many major advances in the study of migration and dispersal have come from avian studies. Second, technologies that are small and versatile enough to track small birds should allow for the movements of most other vertebrates – and even some large invertebrates – to be followed.

In a nutshell:

- Technological advances in tracking and sensing devices have greatly facilitated the study of migratory animals
- Because most migratory animals are physically too small to be tracked with existing technology, smaller, longer lasting devices need to be invented
- Combining sensors with tracking devices promises to better explain the physiological and behavioral challenges that animals face during migration
- Such technological advances will increase the current understanding of migratory animals, thereby revolutionizing future conservation efforts

Birds have been the subject of many conceptual advances in behavior, ecology, and evolutionary biology, yet their mobility has also inhibited progress toward understanding many fundamental biological processes. Factors that influence regulation of population sizes, for example, involve events that occur over the full annual cycle. Identification of the relationships among, and relative importance of, events – on the breeding grounds, en route during migration, and in the wintering range – is fundamental to the effective conservation and management of migratory animals. However, these data are rare, because of the difficulties of following highly mobile individuals.

Researchers can now study animal movement across broad spatial and temporal scales, using several remote-sensing technologies (Table 1). These provide diverse options for assessing the behavior, ecology, and physiology of migratory birds. In this paper, we review the ways in which these technologies have been used to overcome the limitations of methods used in previous studies of animal migration. We discuss four major topics in animal migration studies that show particular promise of rapid

[1]*Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR* *(douglas.robinson@oregonstate.edu); [2]*Department of Theoretical Ecology, Lund University, Lund, Sweden*; [3]*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ*; [4]*Computational Geo-Ecology, Institute for Biodiversity and Ecosystem Dynamics, Universiteit van Amsterdam, Amsterdam, Netherlands*; [5]*Zoological Museum, University of Copenhagen, Copenhagen, Denmark*; [6]*Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, MS*; [7]*Biology Department, Boston University, Boston, MA*; [8]*Environmental Studies Program, Hiram College, Hiram, OH*; [9]*Museum of Vertebrates and Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY*

advances in knowledge because of ongoing technological and analytical developments.

■ Migratory connectivity

How migration and other factors connected with breeding and wintering grounds influence population dynamics remain major unanswered questions in biology, largely because of an inability to track individuals throughout their annual cycle. Many migratory bird species have experienced marked changes in population over the past few decades, but because researchers do not know how and where the populations are regulated, efforts to manage and conserve these species have been hampered. The missing link in efforts to understand mechanisms of population regulation is due to a lack of knowledge regarding where specific individuals breed and overwinter. Initial attempts to link breeding and wintering sites involved placing leg bands on birds captured at one site and hoping for a recapture elsewhere (Figure 1). Despite annual marking of millions of songbirds, however, recoveries have been rare. More than one million pied flycatchers have been banded in Europe, for example, but only six have been recovered on their African wintering grounds (Webster *et al.* 2002).

More recently, connecting breeding, wintering, and migration routes of birds has involved two different approaches. In one approach, individuals may be assigned to likely regions of origin based on broad-scale associa-

Table 1. Technologies being used to study animal movement

Technique	*Distances tracked (short, medium, long)*	*Uses*	*Limitations*	*Examples*
Chemicals (isotopes) in tissues	Short–long	Assign approximate locations where individual birds molted feathers	Coarse spatial resolution. In North America, north–south resolution better than east–west. Also tends to vary with altitude and elevation, and may vary considerably within single site. Maps for other locations are less "finished" than the North America map. Maps may also vary from year to year.	Hobson and Wassenaar (2008)
Genetic markers	Short–long	Assign individuals to populations based on different genetic markers	Limited genetic differentiation in many species reduces ability to establish locations.	Lovette *et al.* (2004)
PTT tags (RFID; Radio Frequency Identification)	Short	Identify a marked individual with a reader placed at a strategic location (feeding or nesting site)	Readers are expensive and must be placed within a few meters of a nest or feeding site.	Local movements of birds to and from feeding stations
Radio (VHF; Very High Frequency) telemetry	Short–medium (long in rare situations with certain landscapes and extraordinary effort)	Provide an individual animal's location, relay physiological data gathered from sensors	Transmission distance relatively short to ground-based receivers. Battery life of small transmitters a few weeks. Transmitter may also influence animal behavior.	Cochran *et al.* (2004); Thorup *et al.* (2007)
Geolocators	Medium–long	Use day length to estimate latitude and longitude; primarily used on seabirds, but now small enough for medium-sized passerines	Spatial resolution varies seasonally across globe. Must recapture smaller animals to retrieve data.	Burger and Shaffer (2008)
Satellite telemetry	Short–long	Track larger animals across globe	Unless combined with GPS, accuracy can be low. Expensive to access data. Minimum size (about 8 g, 22 g with GPS) still too large for many species.	Many studies: Beekman *et al.* (2002); Thorup *et al.* (2003); Berthold *et al.* (2004)
Radar	Short	Track intensity, speed, and direction of migration; track short flights of individuals	For most systems, there is no individual- or species-specific information. Low flying birds may be missed.	Bruderer (1997); Gauthreaux and Belser (2003)

Note: Technologies being used to study animal movement vary in their usefulness and limitations. Ideal devices would be small enough to be carried by the smallest migratory organisms without affecting behavior, allow long-distance tracking with great precision and minimal researcher effort, and measure characteristics of the organism and the environments through which the organism passes as it migrates. No currently available technology meets all these goals, but advances can still be made by careful selection of current technology. PTT = Platform Transmitter Terminal.

Figure 1. *Technology has improved our abilities to track and study migratory birds. Simple early techniques, such as bird banding, relied on capturing individuals, marking them with uniquely numbered metal leg-bands at one location, and then recapturing those marked individuals at another location to identify destinations. Technology has advanced through time – from short-distance tracking by directly following radio-tagged birds, to radar detection of large-scale bird migrations, to methods that rely on satellite telemetry or chemical analysis of feathers. In the future, better use of cellular communications networks will further refine tracking.*

tions across large geographical areas. Current techniques include examination of morphological variation in physical characteristics, such as plumage color, composition of chemicals in feathers, and geographically specific genetic markers. Unfortunately, most migratory species possess insufficient morphological and genetic variation for such an approach to be useful (Lovette *et al.* 2004). The second approach relies on chemical analysis, comparing ratios of isotopes of common elements in bird tissues with isotopic ratios in the environment via a geographic map (Hobson and Wassenaar 2008). However, identification of source areas of individual birds has been at a very coarse level, being limited to assignment within large geographic regions, such as the eastern Caribbean or the southern United States (Rubenstein *et al.* 2002). Furthermore, some elemental ratios vary so widely with altitude, as well as with age of individual birds, that local variation often approximates variation across continental scales (Graves *et al.* 2002). This method is therefore currently too limited to identify the specific breeding and wintering sites of individual birds. Recent efforts to combine isotopic analyses with genetic analyses show promise for narrowing identification of the possible sites (Clegg *et al.* 2003), yet pinpointing positions to key areas of environmental concern still seems out of reach. Ideally, the most effective way of gaining this information will come from the second approach – tracking individual organisms throughout their annual cycle. Recently developed technologies are enabling researchers to collect more precise data on an increasingly wide array of species.

In the past few years, advances in long-distance tracking devices have included satellite telemetry, which follows individual birds – fitted with tracking units powered by batteries or solar panels – via the Global Positioning System (GPS) satellite network (Cohn 1999). Such devices have revealed hitherto unknown global migratory patterns of oceanic birds (Shaffer *et al.* 2006), linked breeding with wintering sites in many species of larger birds (eg waterfowl), and helped to answer conceptual questions about the navigational abilities and physiology of birds during migration (Alerstam 2006). In addition, geolocators, which sense photoperiod and time of sunrise and sunset, have been used to estimate the approximate latitude and longitude of migrants (Burger and Shaffer 2008; Stutchbury *et al.* 2009). Answers to important questions for understanding avian movements – previously impossible to address, yet necessary to advance our knowledge of both basic and applied arenas – are now within reach. We encourage researchers already using satellite telemetry to do more than "connect the dots" by mapping migration routes, but also to use these opportunities to study factors influencing migratory performance and evolution of migratory behavior. One serious drawback remains: most devices are too large for the majority of migratory species, whose individual masses fall between 5 and 200 g. Size reduction of tracking technologies will open a new frontier in migratory connectivity studies, not just for birds, but possibly for even smaller organisms, such as insects (Holland *et al.* 2006).

■ In-flight behavior and dynamic spatial demography

Studying avian behavior during flight poses particular technical challenges, because most migration occurs at night, often at high altitudes, and a bird's presence within range of the monitoring technologies is fleeting. Researchers studying the in-flight behavior of birds too small to carry satellite tags generally either follow birds with radio transmitters or monitor individuals passively as they pass through the observational fields of portable radars (radio detection and ranging), thermal imagers, or acoustic microphone arrays.

Much of the research on in-flight behavior focuses on birds' movement patterns and their responses to immediate circumstances and conditions. Inexpensive "marine" radars and thermal imagers are used to measure height distributions, especially in relation to determining hazards posed by anthropogenic structures (Desholm and Kahlert 2005). Biological tracking radars are considerably more expensive, scarce (ie very few have been produced to date), and difficult to maintain, but the detailed information they yield on the movements of individual birds has provided new insights into how birds orient (Alerstam *et al.* 2001) and respond to weather and terrain (Bruderer and Liechti 1998). Weather radars sweep through large volumes of airspace and record broad spatial distributions of birds and other biological "targets" (Larkin 2005). These radars have proven useful in identifying important stopover habitats (Gauthreaux and Belser 1998), mapping large-scale spatial structure, and determining responses to migratory barriers (Diehl *et al.* 2003).

The scale and comprehensiveness of weather radar coverage in the US mean that in some cases it may be possible to track demographic changes in large proportions of entire populations (eg roosting swallows; Figure 2), because an entire continent can be monitored. Gauthreaux (1992) detected large fronts of migrating birds that suggest year-to-year variation in the volume of migrant traffic. Such a system raises the possibility of truly dynamic spatial demography of some species, discerning their movements and mortality and, when combined with other data sources, assessing annual variation in the effects of weather and habitat availability on the migratory movements and levels of mortality in populations. In the near future, modified weather radar systems will record even more information on biological targets, including data on reflectivity, radial velocity, and spectral width at fine resolutions. This capability will increase our ability to understand, for example, habitat use during migration in real time and for large numbers of birds; local movement patterns, such as daily foraging flights of waterfowl and blackbirds; and decision-making processes of migrating birds as they encounter topographic obstacles such as mountains.

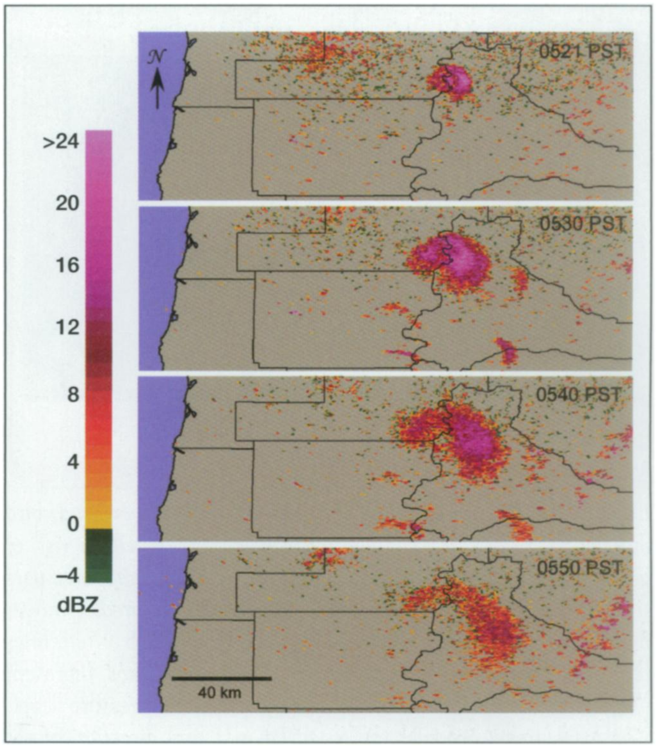
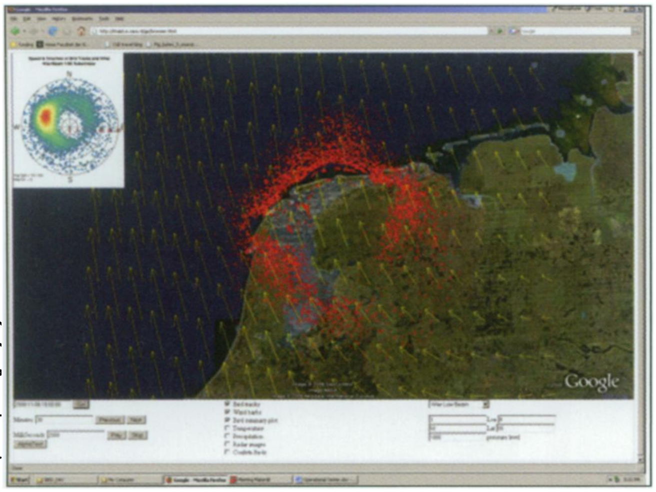


Figure 2. *Radar can detect roosts of migratory birds, such as barn swallows (*Hirundo rustica*), which are shown here departing their night-time roost in a cornfield north of Corvallis, Oregon, on 4 Sep 2008. As birds begin to depart the roost early each morning during autumn, their radar echoes expand in area as the birds move away from the roost site. This technology could be used to locate many, if not most, of the swallow roosts across the US and to estimate the total continental population sizes of these migratory species. dBZ = decibels of Z; PST = Pacific Standard Time.*

Behavior and ecology of movement

Diverse techniques are used to study various behavioral aspects of migration, such as orientation, navigation, timing, routes and speeds, travel decisions, and stopover site selection. Early studies used either mark–recapture or laboratory methods to investigate migratory behavior, because of the difficulties associated with following individuals in the field (Alerstam 2006). Despite limited information on individual behavior, large-scale banding studies have provided insights into the timing of migration, as well as effects of weather and other large-scale processes on the behavior of migrants.

Meteorological conditions can have a major impact on migratory behavior. Specifically, the influence of wind speed and direction on migration intensity, departure decisions, and flight altitude has been studied by means of various techniques. Mark–recapture data have been used to look at annual variability in phenology and population size in relation to local or large-scale weather patterns, such as the North Atlantic Oscillation (Huppop and Huppop 2003). Daily and annual variations in migration intensity have been attributed to meteorological conditions for several species, based on visual observations as well as radar (Gauthreaux and Belser 2003), and predictive migration models based on this relationship have been developed to reduce collisions of birds and aircraft (van Belle *et al.* 2007; Figure 3). Using satellite telemetry, researchers have studied the influence of meteorological conditions along the migration routes for several species and how this varies between individuals, seasons, or regions (Fox *et al.* 2003; Thorup *et al.* 2003). Different



European Space Agency FlySafe Initiative

Figure 3. *By combining information on weather and bird movements, researchers can provide warnings to reduce risk of bird and aircraft collisions. Here, the Netherlands Air Force uses surveillance radar in Wier, The Netherlands, to predict movements of birds toward the UK on 6 Nov 2008. Red lines represent short bird trajectories, and yellow arrows represent wind strength and direction at the 925-millibar pressure level. The inset image provides the speed (m s^{-1}) and direction of the tracks, with higher intensities indicated in red.*

tracking techniques have also been used to show a relationship between flight altitudes of soaring birds and thermal convection (Shannon *et al.* 2002). Furthermore, the link between migration timing at distant locations and weather on breeding grounds can be modeled by integrating meteorological data with tracking and observational data (Shamoun-Baranes *et al.* 2006).

Simple lab technologies such as "Emlen funnels" – funnel-shaped cages with an open top where birds can see experimentally manipulated versions of the night-time sky – have long been the dominant way of studying migratory orientation in birds (Berthold 2001). Migratory birds, placed in the funnels at night, tend to jump in the direction that free-flying migrants would normally move. Scratches from a bird's feet left on the inside of the funnel provide an indication of the individual's preferred direction. Similar methods for testing the orientation of individual animals have only recently been developed for other migratory animals – for example, turtles (Lohmann 1991) and butterflies (Mouritsen and Frost 2002). Funnel studies have been combined with data from radar, and more recently from lightsticks (phosphorescent material attached to the tail or lower back of bird so its direction of flight can be seen as it departs into the night) and ceilometers (powerful beams of light pointed into the sky; Zehnder *et al.* 2001), enabling researchers to follow individual behaviors in nature for a short period. Displacement experiments, which involve the capture and translocation of individuals off their usual migration route, with subsequent study of how animals shift migratory direction and timing, still form the basis of our current understanding of the orientation and navigation of free-flying birds (Perdeck 1958; Mewaldt 1960). Orientation and navigation have also been studied via conventional radio telemetry (Cochran *et al.* 2004; Thorup *et al.* 2007) and satellite telemetry (Luschi *et al.* 2007).

Telemetry is a useful tool in determining stopover sites and the importance of habitat quality and availability in shaping migration routes. In addition, telemetry has revealed how these stopover sites vary from year to year, based on food availability (Berthold *et al.* 2004) or meteorological conditions (Beekman *et al.* 2002). Radio and satellite telemetry have also been used to determine travel decisions during migration (Åkesson and Hedenström 2000; Thorup *et al.* 2007).

■ Physiological ecology of migration

Many life-history tradeoffs of migrants are mediated at the physiological level. One of the most spectacular examples of a physiological tradeoff during bird migration involves the atrophy of digestive and other organs during long migratory flights over ecological barriers (McWilliams and Karasov 2001). Great strides have also been made recently in understanding life-history tradeoffs in immunology, predation, and refueling ecology (Schmaljohann and Dierschke 2005; Williams *et al.* 2007) during migratory stopovers. These recent methodological advances will allow for some of the inherent limitations of previous studies that used only passive mist-netting or banding.

With remote sensing, studies can now be performed in the field that otherwise would have been consigned to the laboratory or the wind tunnel. For example, radio transmitters allow researchers to repeatedly and consistently locate birds in stopover habitats (Bachler and Schaub 2007). Radiotracking also permits us to test hypotheses better than passive mistnetting would allow, because the former method increases the chances of recapturing or observing free-flying birds again. Furthermore, the physiology of free-flying birds may now be ascertained through remote measurements, such as those of blood metabolite concentration (Williams *et al.* 2007).

No longer limited to studying birds at a single stopover site, scientists can now follow individual birds throughout multiple migratory flights and take physiological measurements when a given bird is airborne or on the ground (Ward *et al.* 2002; Bowlin *et al.* 2005; Figure 4). By allowing the physiological consequences of, for example, migrating in certain weather conditions to be measured, much more information about how climate change may affect migratory birds could be obtained (Bowlin and Wikelski 2008). Transmitters and other biosensors can now measure parameters including, but not limited to, heart rate, wingbeat frequency, respiration, and blood chemistry. Physiological and behavioral test subjects need not have to migrate in the unnatural confines of a wind tunnel for study purposes; such information may be captured from birds in the wild. For example, avian heart rate can be used as a direct and continuous measure of stress responses to changing environmental conditions and could therefore help identify

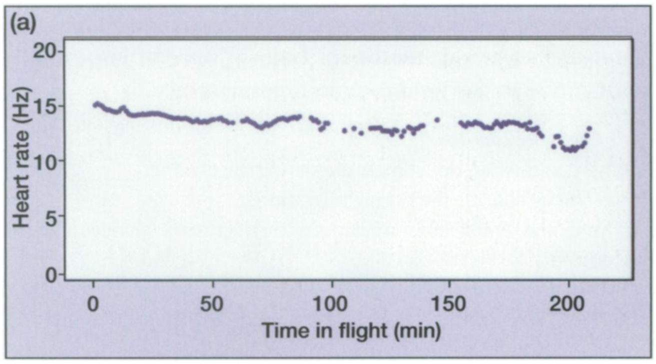


Figure 4. *(a) Example of physiological measurements from a migrating Swainson's thrush* (Catharus ustulatus)*. This graph shows the heart rate (averaged by minute) of a free-flying Swainson's thrush migrating over Illinois. The bird flew ~3.5 hours from Champaign, Illinois, to near Lake Bluff, Illinois, on the shores of Lake Michigan. These data were obtained with a special radio transmitter that allowed researchers to count each heart beat of the bird while it was flying, as long as it was in range of the receiver. Later, researchers were able to use the bird's heart rate to calculate its rate of energy expenditure during the flight (Bowlin and Wikelski 2008). (b) A similar unit is shown on the back of this white-eyed vireo* (Vireo griseus)*.*

potential stressors, such as predators, storms, and human-related disturbances at stopover sites or during migratory flights. Such data can lead to important conservation measures that would have otherwise been difficult to develop, resulting from researchers' inability to continuously monitor avian physiology in field settings.

The spatial and temporal scale currently available for remote physiological monitoring varies with bird size. Large data loggers (~20 g) can store continuous data on heart rate, body temperature, and other parameters for up to several months, over any spatial scale. The main drawback to the use of such loggers is that the animal must be recovered in order to retrieve the data. For small birds, current physiological tracking capabilities are limited to a temporal scale of 5–10 days and two to three migratory flights. However, recording devices continue to be miniaturized, and scientists will eventually be able to obtain physiological measurements from small birds throughout the annual cycle, just as can now be done with large birds.

Remote physiological sensing during migration will also help to resolve other outstanding questions – for example, whether birds initially experience a decline in physical condition upon arrival at a stopover site or whether this decline is a handling-related effect due to capture and banding. Data from natural, uninterrupted migration, as well as information about physiology during multiple flights and stopovers for each individual bird, will be able to be obtained. Moreover, scientists might also be able to use remote sensing to determine when and where mortality occurs during migration.

■ Combining approaches

Our understanding of bird migration would be greatly improved by combining different tracking technologies, to provide insight at different scales (in space and time, from individuals to populations), and by taking advantage of advances in computer sciences, informatics, and analytical techniques to integrate different data sources (Table 2).

In the near future, studies in which animals are followed throughout their entire life cycle, in their natural environment, may be possible. Smaller-sized transmitters will be important in this respect, because they will allow research on smaller species with shorter life spans, as well as to facilitate collection of larger samples (Wikelski *et al.* 2007). Engineering of miniature devices and smaller, long-lasting batteries continues, thanks in part to market pressure for electronic communication gadgets. Size reductions of integrated circuits, increased memory, and provision of stable, lightweight power sources for such devices provide opportunities to adapt these advances for tracking purposes. Studies using smaller and better technology will allow inference about the long-term costs of migratory behaviors and will allow for a more complete understanding of seasonal carry-over effects. The possibility of prolonged tracking of individuals will also make it feasible to further the experimental study of movement behavior, which is essential for a full understanding of the behavioral mechanisms underlying migration.

■ Summary

In this review, we have outlined four major areas in animal movement studies that have benefited from existing technologies. Such technological advancements include radio telemetry (physiology and behavior), radar (demography and behavior), measurement of stable isotopes in feathers (connectivity), and satellite telemetry (connectivity and behavior), all of which have greatly expanded existing

Table 2. Technological improvements required to advance each of the four major topics in studies of migration

(1) Migratory connectivity
Ability to follow many animals of all sizes on a global scale
Ability to distinguish if a tracking unit has failed or fallen off, or if the animal has died, which will improve estimates of mortality during migration
Combining stable isotopes and genetic markers with better resolution to provide simultaneous east–west and north–south resolution of potential breeding location
(2) Behavior and ecology of movement
Invention of small transmitters that can measure cues in the environment (olfactory, geomagnetic, light levels, etc) that birds may be using to orient or navigate
Ability to manipulate these cues in free-flying, naturally migrating animals
Improved access to Earth observation data
Invention of small transmitters that can measure atmospheric conditions while birds are migrating
Expansion of observation networks (ie more radar and banding sites)
Improvement of automated radar target identification
(3) In-flight behavior and dynamic spatial demography
Ability to measure altitude of flight, especially in combination with known global positions
Ability to determine where and when mortality occurs
Ability to quantify spatial density distributions on a large scale
(4) Physiological ecology of migration
Ability to remotely measure more physiological parameters, for longer periods of time, on a global scale, on increasingly smaller animals
Ability to perform blood tests remotely

Note: For all topics, more data are needed to increase sample sizes for a particular species or population, the number of species monitored, or the spatial and temporal resolution of measurements.

Table 3. Although we know more about migration and animal movement than ever before, several important questions in the field remain unanswered

(1) Migratory connectivity
Where and when do animals die during migration?
How many animals die during migration?
Where and when are populations of migratory animals regulated?
(2) Behavior and ecology of movement
How do animals orient during migration?
How do animals determine where they are on the globe during migration?
How will climate change affect migratory animals?
How does stopover habitat quality affect birds' migratory decisions and success?
How do local responses to environment affect large-scale movement patterns?
(3) In-flight behavior and dynamic spatial demography
How far do young migratory animals disperse from their natal territories?
Where and when do animals die during migration?
What factors prompt dispersal to a new breeding site in adults and juveniles?
(4) Physiological ecology of migration
What physiological strategies do animals use to minimize energy costs during migration?
How and why do the costs of migration vary among individuals and species?
Do birds begin gaining weight immediately upon landing in stopover habitat?
What physiological tradeoffs occur during migration, and how do these tradeoffs come about?

knowledge on the biology of bird migration. Although many important questions remain (Table 3), it should be possible to answer these either through combinations of existing technologies or by the development of new technologies, which we hope will become available to researchers within the next 5–10 years.

Data increasingly show that survivorship of many bird species is lowest during the migratory phase of the avian life cycle (Sillett and Holmes 2002), but what is the reason for this mortality? Do anthropogenic effects (eg tall structures, land use, climate change) aggravate the impact of natural hazards on migratory birds in ways that have consequences for the health of populations? Is avian mortality associated with anthropogenic intrusions on the landscape and airspace additive or compensatory? How do events outside the breeding season influence reproductive success? Advances in electronics-based technologies, the use of radioisotopes, and genetics will go far toward addressing these and other questions that have remained unanswered (or unanswerable) for many years.

■ Acknowledgements

MIGRATE, a research coordination network funded by the US National Science Foundation (NSF), facilitated our collaboration. Additional support was provided by NSF grants #0454822 (to WDR) and #0352925 (to DWW).

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