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Front Ecol Environ 2009; doi:10.1890/080179

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Integrating concepts and technologies to advance the study of bird migration

W Douglas Robinson1*, Melissa S Bowlin1, Isabelle Bisson2, Judy Shamoun-Baranes3, Kaspar Thorup1, Robert H Diehl6, Thomas H Kuntz2, Sarah Mabey9, and David W Winkler9

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.

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

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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.

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
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 expe-
rienced 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 reg-
ulation is due to a lack of knowledge regarding where spe-
cific 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 recap-
ture elsewhere (Figure 1). Despite annual marking of mil-
ions 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 the 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>
<thead>
<tr>
<th>Technique</th>
<th>Distances tracked</th>
<th>Uses</th>
<th>Limitations</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chemicals in tissues (isotopes)</td>
<td>Short–long</td>
<td>Assign approximate locations where individual birds molted feathers</td>
<td>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.</td>
<td>Hobson and Wassenaar (2008)</td>
</tr>
<tr>
<td>Genetic markers</td>
<td>Short–long</td>
<td>Assign individuals to populations based on different genetic markers</td>
<td>Limited genetic differentiation in many species reduces ability to establish locations.</td>
<td>Lovette et al. (2004)</td>
</tr>
<tr>
<td>PTT tags (RFID; Radio Frequency Identification)</td>
<td>Short</td>
<td>Identify a marked individual with a reader placed at a strategic location (feeding or nesting site)</td>
<td>Readers are expensive and must be placed within a few meters of a nest or feeding site.</td>
<td>Local movements of birds to and from feeding stations</td>
</tr>
<tr>
<td>Radio (VHF; Very High Frequency) telemetry</td>
<td>Short–medium (long in rare situations with certain landscapes and extraordinary effort)</td>
<td>Provide an individual animal’s location, relay physiological data gathered from sensors</td>
<td>Transmission distance relatively short to ground-based receivers. Battery life of small transmitters a few weeks. Transmitter may also influence animal behavior.</td>
<td>Cochran et al. (2004); Thorup et al. (2007)</td>
</tr>
<tr>
<td>Geolocators</td>
<td>Medium–long</td>
<td>Use day length to estimate latitude and longitude; primarily used on seabirds, but now small enough for medium-sized passerines</td>
<td>Spatial resolution varies seasonally across globe. Must recapture smaller animals to retrieve data.</td>
<td>Burger and Shaffer (2008)</td>
</tr>
<tr>
<td>Satellite telemetry</td>
<td>Short–long</td>
<td>Track larger animals across globe</td>
<td>Unless combined with GPS, accuracy can be low. Expensive to access data. Minimum size (about 8g, 22g with GPS) still too large for many species.</td>
<td>Many studies: Beekman et al. (2002); Thorup et al. (2003); Berthold et al. (2004)</td>
</tr>
<tr>
<td>Radar</td>
<td>Short</td>
<td>Track intensity, speed, and direction of migration; track short flights of individuals</td>
<td>For most systems, there is no individual- or species-specific information. Low flying birds may be missed.</td>
<td>Bruderer (1997); Gauthreaux and Belser (2003)</td>
</tr>
</tbody>
</table>

**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.
New technologies for migration research

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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 the cellular communications network will further refine tracking.

In-flight behavior and dynamic spatial demography

Studying avian behavior during flight poses particular technical challenges, because most migration occurs at night,
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 have been developed, based on this relationship, 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
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 light-sticks (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 an important 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 stopover. 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 mist-netting 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
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, since 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...
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, and 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.

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

<table>
<thead>
<tr>
<th>(1) Migratory connectivity</th>
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<tbody>
<tr>
<td>Ability to follow many animals of all sizes on a global scale</td>
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<tr>
<td>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</td>
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<tr>
<td>Combining stable isotopes and genetic markers with better resolution to provide simultaneous east–west and north–south resolution of potential breeding location</td>
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<th>(2) Behavior and ecology of movement</th>
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<tbody>
<tr>
<td>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</td>
</tr>
<tr>
<td>Ability to manipulate these cues in free-flying, naturally migrating animals</td>
</tr>
<tr>
<td>Improved access to Earth observation data</td>
</tr>
<tr>
<td>Invention of small transmitters that can measure atmospheric conditions while birds are migrating</td>
</tr>
<tr>
<td>Expansion of observation networks (ie more radar and banding sites)</td>
</tr>
<tr>
<td>Improvement of automated radar target identification</td>
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<th>(3) In-flight behavior and dynamic spatial demography</th>
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<tbody>
<tr>
<td>Ability to measure altitude of flight, especially in combination with known global positions</td>
</tr>
<tr>
<td>Ability to determine where and when mortality occurs</td>
</tr>
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<td>Ability to quantify spatial density distributions on a large scale</td>
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<th>(4) Physiological ecology of migration</th>
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<tr>
<td>Ability to remotely measure more physiological parameters, for longer periods of time, on a global scale, on increasingly smaller animals</td>
</tr>
<tr>
<td>Ability to perform blood tests remotely</td>
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**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.

### References


### 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).


