Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds

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Basic questions about the life histories of migratory birds have confounded scientists for generations, yet we are nearing an era of historic discovery as new tracking technologies make it possible to determine the timing and routes of an increasing number of bird migrations. Tracking small flying animals as they travel over continental-scale distances is a difficult logistical and engineering challenge. Although no tracking system works well with all species, improvements to traditional technologies, such as satellite tracking, along with innovations related to global positioning systems, cellular networks, solar geolocation, radar, and information technology are improving our understanding of when and where birds go during their annual cycles and informing numerous scientific disciplines, including evolutionary biology, population ecology, and global change. The recent developments described in this article will help us answer many long-standing questions about animal behavior and life histories.

Keywords: tracking technology, geolocators, cellular tracking, satellite transmitter, radar ornithology

Approximately 250 years ago in the English village of Selbourne, pioneering naturalist Gilbert White made a simple observation: He noted that a very stable population of eight pairs of common swifts (*Apus apus*) arrived in the summer to breed year after year, whereas for similar species (swallows and martins; family Hirundinidae), the number of breeding pairs fluctuated from year to year. White wondered what might be happening to these birds away from the breeding area that might account for this demographic variation (Lawton and May 1983). In so doing, he articulated a central and important question in population biology: What regulates population sizes? For many migratory bird species, the answer to this question continues to elude us. Without the ability to track the migration routes of birds like swifts and swallows, we lack crucial information about where they go and how they survive outside of the breeding season. Only a comprehensive understanding of migratory life histories will allow us to explain White's observation (Faaborg et al. 2010, Robinson et al. 2010).

Fortunately, the answers are finally within reach with respect to most bird species. Advancements in bird-tracking technology are bringing us closer to addressing White's inquiry, along with many other questions about migratory life histories. Miniaturized GPS (global positioning system) devices can generate location data with unprecedented accuracy for some species (Kotzerka et al. 2010, Paiva et al. 2010), and new satellite technology (e.g., the

International Cooperation for Animal Research Using Space [ICARUS] project) is under development that will provide global tracking data for a wealth of understudied species (Wikelski et al. 2007). Tracking devices weighing less than a gram (g) are now in use and will allow us to map the individual movements of small songbirds (which constitute the majority of bird species) for the first time. Also, biologists and engineers are finding new ways to exploit other technologies, such as cellular networks, weather surveillance radar, and cyberinfrastructure, to help us monitor the movements of migratory animals.

Studies of migration address a great diversity of questions in a number of different fields (Dingle and Drake 2007, Bowlin et al. 2010a). A physiologist may focus on the sensory and biochemical mechanisms that allow a migrating bird to travel across the globe (McWilliams et al. 2004, Guglielmo 2010, Thorup et al. 2010), whereas an evolutionary biologist may focus on life-history tradeoffs associated with the costs and benefits of long-distance travel (Boyle and Conway 2007, Jahn et al. 2010). However, virtually all efforts to study migration rely on some form of tracking data, which can be difficult to obtain for many migratory birds. Although most migratory birds are small (less than 30 g; see figure 1), they travel distances on the order of hundreds or thousands of kilometers (km), which creates a challenging engineering problem for researchers. Any signal-transmitting tracking device deployed on an animal must be small enough that
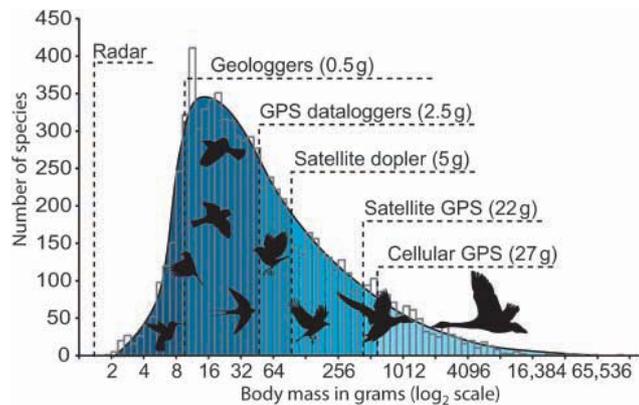
Figure 1. The frequency distribution of bird body masses (in grams) in relation to possible tracking technologies. Minimum bird sizes for each technology are represented according to the 5%-body-weight rule.

the animal can carry it without difficulty, yet it must emit enough energy to be detected, which requires an adequate power supply. Although battery technology has improved over the years, batteries capable of powering long-distance transmission for long periods are still too heavy for small birds. There is some debate about the appropriate sizes for devices borne by flying birds. Most experts suggest a rule of thumb of 3%–5% of an animal's body weight (Murray and Fuller 2000; Barron et al. 2010), whereas others emphasize minimizing the size or profile of tracking devices (Caccamise and Hedin 1985, Bowlin et al. 2010b). Even the most liberal guidelines will impose serious restrictions on tag size; therefore, we will need to continue to find innovative ways to miniaturize devices while increasing their functionality.

Recent reviews, including those in the February 2007 issue of *BioScience*, have described new avenues of research made possible by advancements in tracking technology (Bowlin et al. 2010a, Robinson et al. 2010). As a supplement to these efforts, we present a practical guide to some of the emerging technologies in the field of animal tracking that includes notes about the nature and quality of the data they provide and the cost of implementation (table 1). Tracking technologies may be classified either by the way they derive location data (e.g., GPS receivers, solar geolocation, Doppler shifts detected by satellites) or by the way in which we obtain the data (e.g., satellite uplinks, ground-based receivers, retrieving

Table 1. Some key properties of bird-tracking technologies.

Data retrieval system	Tracking technology	Minimum device mass (grams)	Minimum cost per unit (US dollars)	Maximum locations per day	Resolution/accuracy (best expected, in meters)	Range of operation
Satellite relay systems (data collected by and retrieved from satellites)	Doppler effect	5	4,000	1	150	global
	GPS	22	4,000	approximately 20	5	global
Ground-based receivers (data retrieved by fixed or mobile antennas)	tower identification	not realized	unknown	approximately 10	approximately 30,000	approximately 80% terrestrial?
	GPS/GSM	27	2,500	>2000[1]	5	global[2]
	radio telemetry	0.3	250	approximately 200	100	local (or mobile)
	GPS logger with transmitter	18	1,200	>100[1]	5	global[2]
	solar geolocator with transmitter	not realized	unknown	2	approximately 200,000	global[3,4]
Dataloggers (require recovery of the tracking device)	GPS	2.5	700	>100[1]	5	global
	solar geolocation	0.5	approximately 100	2	approximately 200,000	global[4]
Radar	marine radar, X-band radar	not applicable	variable[5]	>1000	5	local
	weather surveillance radar	not applicable	free	approximately 144	500	North America and Europe

[1]Depends on battery size.
[2]Capable of logging location data globally, but the transmission of data can only occur where there is cellular coverage.
[3]Local download.
[4]Accuracy is limited in equatorial areas during some parts of the year and in polar regions.
[5]The cost for X-band tracking can vary from approximately $25,000 for equipment rental and postprocessing to $250,000 for the purchase of an assembled radar and data analysis. Specialized tracking radar equipment or other high-end portable systems can cost as much as $1,000,000.
GPS, global positioning system; GSM, Global System for Mobile Communications

the tracking device itself). In this review, we have organized tracking methods into sections according to the four primary means by which researchers obtain data from their devices: (1) satellite relay, (2) ground-based receivers, (3) tag recovery (archival devices), and (4) radar tracking. Finally, we offer a brief discussion of new cyberinfrastructure initiatives that are emerging as important tracking tools.

Satellite tracking

Satellite-based tracking methods are appealing because they permit near-real-time acquisition of location data from tags located almost anywhere on the globe. This feature allows researchers not only to track birds while they are alive but also to determine when and where they die (Strandberg et al. 2010), so long as the tags remain functional. The main disadvantages associated with satellite systems are the high cost and the power requirements. Satellites are expensive, and the low-orbit satellites that work best for tracking systems have a relatively short life span. Even with a low-orbit system, a ground-based transmitter must typically be able to transmit over distances of about 2300 km to reach the satellite. For a comparison, cellular systems usually operate over distances of up to 50 km. Therefore, the power needed to send a signal to a satellite is relatively high, which requires a relatively large battery. The smallest satellite tags currently available have a mass of about 5 g, most of which is battery.

The simplest satellite-based devices use the Doppler shift in pulsed radio frequencies to locate transmitters (Maxwell 1971). When a satellite receiver first detects a ground-based transmitter, the perceived frequency emitted by the transmitter is higher than the actual transmission frequency, because the satellite is rapidly approaching the transmitter. The perceived frequency then progressively decreases as the satellite approaches the transmitter and passes over it, at which point the Doppler shift goes from positive to negative, marking the position of the transmitter along a line parallel to the flight path of the satellite (see figure 2).

As the satellite passes over the transmitter, the relative velocity between the tag and the satellite changes with the cosine of the angle between the satellite trajectory and line between the satellite and the transmitter. This angle varies with both the movement of the satellite and the degree to which the transmitter is offset from the flight path of the satellite. If the transmitter is positioned far off to one side of the satellite track, the rate of change in relative velocity is small relative to when the satellite passes directly overhead. The rate of change of frequency that results from this variation in relative velocity is what allows the determination of the location of a transmitter along a line perpendicular to the flight path of the satellite (see figure 2).

With this system, the accuracy of the location data is dependent on the accuracy of the frequency-shift measurement. Errors in this system can arise from several sources, including temperature effects on the oscillation frequency of a transmitter and multipath interference in the transmitted
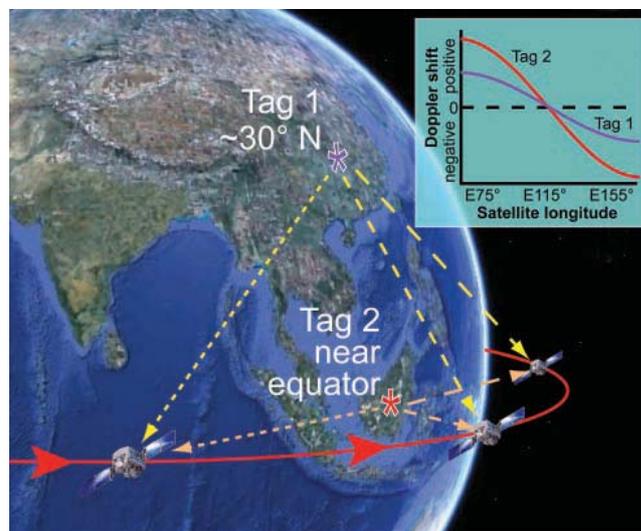

Figure 2. Hypothetical arrangement of a tracking satellite in equatorial orbit and two satellite transmitters (tags 1 and 2), both located at longitude 115° east. As the satellite moves west to east, it passes directly over tag 2 and receives the Doppler-shift signal shown in red on the graph. The satellite passes to the south of tag 1 such that the change in the relative velocity between tag 1 and the passing satellite is less than that between the satellite and tag 2, which gives rise to a more dampened Doppler shift. The location of each tag can be determined by the position of the satellite when the Doppler shift is zero and by the degree to which the Doppler shift changes as the satellite passes by (i.e., the slope of the curve where the Doppler shift is zero).

signal. Accuracy has been reported to vary from about 100 meters (m) to about 50 km (Keating et al. 1991, Vincent et al. 2002, White and Sjoberg 2002, Dubinin et al. 2010).

More advanced tags may modulate the transmitter frequency to deliver data such as temperature, battery voltage, and GPS position. Tags that generate and transmit GPS locations are capable of generating highly accurate (<5-m resolution) and more frequent location data. The downside of these devices is that they require additional power and electronics. The lightest currently available satellite tag with GPS capability weighs 22 g, which limits its use to species weighing about 450 g or more (about 15% of bird species; see figure 1).

Although several companies provide satellite tracking services, most of them require transmitters weighing several hundred grams. The only satellite service provider relevant for bird tracking is Argos (*www.argos-system.org*), and at least five companies make Argos transmitters small enough to use on large birds (see figure 1 and supplementary table S1 online at *http://dx.doi.org/10.1525/bio.2011.61.9.7*). The cost for satellite tracking entails both the cost of a transmitter (roughly $1000–$3000) and the fees for data acquisition (approximately $1000–$4000, depending on the amount of data).

Even with tags weighing 5 g, the Argos system is not optimized for bird tracking. In 2014, the European Space Agency plans to launch the ICARUS project, which aims to deploy a satellite-based sensor system specialized for receiving signals from very small transmitters. The technical requirements for this system are very low orbit altitudes (about 400 km, as opposed to the 850-km orbit of the Argos system) and specialized antennas tuned to receive weak signals from the ground. With such a system, transmitters as small as 1 g could be used to track small birds and even some insects (Blackburn 2006, Wikelski et al. 2007).

Ground-based receivers: VHF and cellular systems

Traditional tracking systems with ground-based receivers (e.g., radio telemetry systems) entail short-range VHF (very high frequency) transmitters and antennas mounted on towers, vehicles, or field assistants. The simplest VHF transmitters emit pulses of energy at a particular radiowave frequency. Multiple tags can be tracked in the same area by using different frequencies and pulse patterns. Generally, a limited number of receivers are used in a given project, and a receiver must be within a few kilometers of a transmitter, depending on the equipment and the environment, to detect it. Therefore, these systems are not capable of tracking migratory birds over long distances unless someone expends the tremendous effort to follow an animal with a mobile antenna (e.g., Cochran et al. 1967, Cochran 1987, Cochran and Wikelski 2005, Bowlin and Wikelski 2008). Nevertheless, VHF transmitters are still used to study migratory birds, and they have achieved new levels of sophistication and miniaturization. The smallest transmitters now weigh less than 0.3 g and have been used on species as small as hummingbirds (Hadley and Betts 2009). Furthermore, modern transmitters can relay information from sensors that provide information about the physiology or activities of the tagged animal, such as heart rate, body temperature, or wing flap rate (Bowlin et al. 2005, Bowlin and Wikelski 2008, Cochran et al. 2008). Prices for VHF tags are relatively low (roughly $150–$300 per transmitter, depending on their capabilities), and published designs are available for building them (e.g., Naef-Daenzer et al. 2005). However, VHF tracking also requires receiving equipment, which generally adds a one-time purchase of several thousand dollars to the price of implementation.

Some ground-based receiver systems incorporate both a geolocation system and a radio communication system whereby stored location data can be obtained using a brief, short-distance transmission. For a migratory bird, the strategy behind this sort of device is to tag birds at a regular breeding or wintering area, have the device log location data during the course of a migratory cycle (either with a GPS module or through solar geolocation), and then initiate a transmission after the animal returns to the area where it was tagged. One or more ground-based receivers would, of course, be in place to receive the signal with a year's worth of

encoded location data. A few companies (see table S1) provide tags weighing on the order of 10 g that can record GPS locations and transmit data via UHF (ultra high frequency) radio emissions. The cost for such devices is around $3000 per tag plus $3200 for a receiver unit.

Ground-based systems often suffer from a limited number of receiver locations. However, recent advances in cellular phone technology and availability have presented migration researchers with a new ground-based receiver system that rivals satellite-based tracking in its detection range. Whereas a satellite transmitter must power a signal over a distance of several hundred to a few thousand kilometers, a cellular device generally transmits a maximum of about 50 km. Therefore, the power requirements for cellular-based tracking devices can be reduced substantially. Of course, cellular networks do not have global coverage, especially in marine environments, which means that reliable mortality data may not be available, depending on where tagged birds die. In addition, users of cellular tracking technologies may encounter difficulties when their tracking devices cross international borders or move among different cellular networks. Over time, these challenges will be reduced as extended networks become more widely available.

Theoretically, the simplest cellular-based tracking device would simply emit a generic transmission signal, and the location of the tag would be determined by identifying the location of a cellular tower with which a successful connection was made. However, not all cellular tower locations can be identified without cooperation from cellular network providers. Therefore, all cellular tracking systems in use today store location data from a GPS receiver and then transmit location data over GSM (Global System for Mobile Communications) networks. Many of these devices feature integrated data-logging and transmission technology, wherein data are gathered, processed, and then stored for a period of time before being transmitted. This functionality permits some power-saving features such as infrequent data transmission that takes place only when reception is adequate. Systems that use a combination of GPS and GSM generally collect altitude data as well as location coordinates, which allows for an unprecedented resolution of flight paths and observations of complex and subtle flight behaviors. For example, these devices have been used to visualize thermal soaring in eagles (figure 3). There is also potential to use animals equipped with GSM systems to serve as environmental probes that relay not only location data but also other sensor data. Such activities are already being carried out in aquatic environments with deep-diving marine mammals (Lydersen et al. 2002).

Combined GPS/GSM devices are still a relatively new technology, and they have yet to achieve the full degree of miniaturization possible. An author of this article (WDR) recently tested a 27-g GPS/GSM device on wild birds, and smaller devices (weighing about 15 g) are under development. As with satellite-based systems, advances in battery and solar power technology will be needed to miniaturize
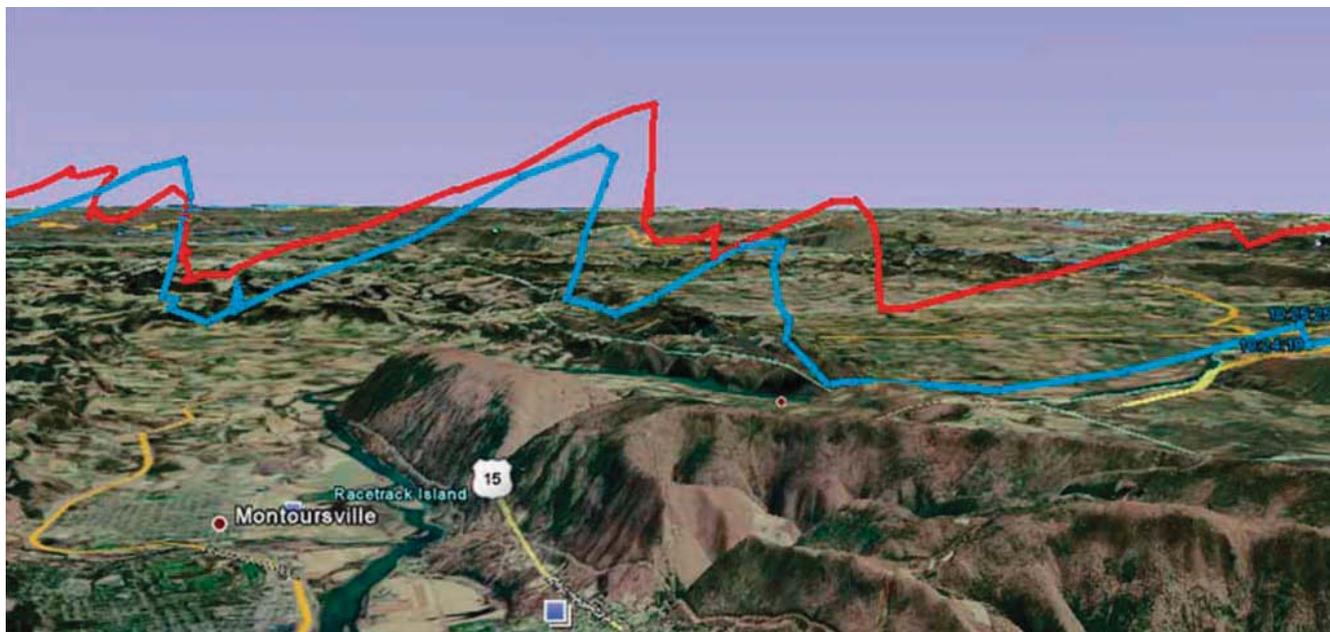
Figure 3. Migratory movements of two different golden eagles passing through central Pennsylvania on different days in autumn 2008, recorded by a CTT-1100 telemetry unit at 30-second intervals. Detailed data of the sort shown here provide a means of in-depth analysis of the behavior and responses of flying birds to variable topography, climate, and human alteration to landscapes. In this case, the data were used to understand how proposed wind farms might affect migratory birds of prey flying along central Appalachian ridges. Of particular interest here is the remarkably similar response by two different birds to the same topographic features. Source: Todd Katzner, Cellular Tracking Technologies, LLC, 2010 (www.celltracktech.com).

GSM transmitters to the point that they can be deployed on small (<30 g) birds. At present, cellular-based tags cost about the same as satellite tags ($1300–$3500), but we expect prices to drop dramatically as they become more widely used. Data acquisition is usually on the order of $300 per year. Suppliers of these devices are listed in table S1.

Archival geolocation devices

One way to reduce the power requirements of tracking devices is simply to dispense with signal transmission. Archival tags or geolocation dataloggers merely store location information for direct retrieval. Of course, these devices require that the tracked animal be recaptured after undergoing a migration cycle. For many species, the chances of recapturing the same individual are miniscule, but for others, a high percentage of individuals return to the same breeding locations year after year, which may allow for at least some geolocation dataloggers to be deployed and later recovered (Stutchbury et al. 2009a).

Two types of geolocation dataloggers are presently used: GPS-based devices and solar geolocation devices. GPS loggers can provide extremely accurate location data and, depending on battery size, can take frequent readings to provide highly detailed movement paths. Power requirements remain an issue for GPS loggers, because a GPS reading requires approximately 0.15 watts over about 30 seconds, but this is considerably less of a drain than continuous

long-distance signal transmission. The smallest such devices weigh approximately 2.5 g and can record about one location per day, so long as the onboard solar charger is exposed to the sun long enough to charge the battery. Unfortunately, availability of these extremely small GPS loggers is limited (see table S1), and they cost around $1000 per unit.

If 2.5 g is too heavy (as is the case for approximately half of all bird species; see figure 1), the only currently available alternative tracking devices are simple radio transmitters (discussed above) or solar geolocation dataloggers (figure 4). Geolocation dataloggers, also called *geologgers* or *geolocators*, are currently the smallest tracking devices that can provide location data for long-distance movements. The simplest geologgers employ a light sensor and an accurate real-time clock to determine the time of sunrise and sunset. Location data are then generated by calculating the length of the day (or night), which indicates latitude, and the time of solar noon, which indicates longitude. Slightly more sophisticated devices may also store altitude or temperature data. Owing to their sheer simplicity, geologgers can weigh less than a gram, and they can be produced for less than $100.

Aside from the need to recapture tagged animals, the primary disadvantage of light-level geologgers is that location data are of relatively low resolution compared with those of other methods. Most geologgers store raw data in the form of a long series of light-level readings taken at regular time intervals. Specialized software is then needed to translate

Figure 4. A painted bunting (approximately 17 grams [g]) in southwestern Oklahoma with a 0.7-g solar geolocation datalogger.

the light data into location data. Usually this software first establishes threshold light levels for estimating the exact time of sunrise and sunset (i.e., particular sun angles). These thresholds are usually based on known location data, which are often taken from the first few days of data collection, during which the bird is assumed to have remained at the release location. The thresholds are then applied to the entire data set to estimate sunrise and sunset times. Obviously, this approach entails some uncertainties. For instance, the behavior of each tagged bird—whether it roosts in cover or in open areas—can affect the light levels detected by a geologger. Furthermore, variation in the landscape over the course of the migration cycle can cause problems—a valley versus a mountaintop, for instance. Efforts are currently under way to incorporate advances in spatial modeling techniques that modify raw coordinates using landscape data (see Sumner et al. 2009) and distribution models (i.e., models that delineate areas that are likely to provide suitable habitat for a species; see Elith et al. 2006).

Presently, geologgers deployed on birds are thought to be accurate to about 200 km with regard to latitude and about 50 km for longitude (Welch and Eveson 1999, Phillips et al. 2004), although these estimates were derived from ocean-going species, which may experience less shading than terrestrial species. The accuracy of latitudinal estimates is strongly affected by the time of year. During the spring and fall equinoxes, when day length is uniform across the globe, it is impossible to determine latitude. Furthermore, latitudinal estimates degrade as a tag approaches the equator, where there is less variation in day length for a given change in latitude. Unfortunately, there have been few validation studies for land-based geologger systems in terrestrial environments, although several are currently under way (Fudickar et al. 2011; Richard Lanctot, Migratory Bird Management Office, US Fish and Wildlife Service, personal communication, 27 April 2011; Steffen Hahn, Department of Bird Migration, Swiss Ornithological Institute, personal communication, 4

May 2011). Although the degree of geologgers' spatial resolution is poor compared with those of GPS devices and satellite transmitters, for many purposes, high-resolution data are not needed. For example, to establish basic connectivity data among regional populations moving between breeding and wintering areas, high-precision coordinates and timing are not necessary.

Very few producers of solar geologgers exist (see table S1). Tags made by the British Antarctic Survey are the most commonly used devices for small birds (see Stutchbury et al. 2009b), with designs weighing as little as 0.8 g. Prices per unit generally range from $100 to $400. Researchers at the Swiss Ornithological Institute (Felix Liechti, personal communication, 27 April 2011) and the University of Oklahoma have independently designed devices weighing as little as 0.5 g and have deployed them on birds that weigh as little as 15 g, at a cost of less than $25 per unit for materials (see figure 3).

Even with their limitations, the potential for geologgers to contribute to the study of bird migration is enormous. More than 40% of migratory bird species are too small for even the smallest satellite- or cellular-based tracking systems. Barring a revolutionary breakthrough in battery technology, geologgers appear to be the only option for tracking small birds over long distances. The current generation of geologgers can be deployed on birds weighing 10 g or more (88% of all bird species; figure 1) according to the 5%-body-weight rule of thumb.

Radar

Radar provides another powerful method of monitoring the large- and small-scale movements of birds and other flying animals. Initially, radar technology was developed primarily for military applications, but biologists quickly realized that radar could do more than track aircraft. Lack and Varley (1945) revealed the potential for radar to detect and study birds, and there have since been many important research efforts that make use of radio wave scattering (bioscatter) to understand airborne animals ranging in size from waterfowl (O'Neal et al. 2010) to insects (Reynolds 1988). Over the past few decades, radar has played a central role in advancing our understanding of how flying animals orient, navigate, distribute themselves in the atmosphere, respond to weather, cope with barriers, and so on. During this period, the sophistication of radar systems has advanced rapidly through the advent of innovative hardware and signal-processing capabilities, thereby creating even more opportunities for using radar in biological research.

Depending on the particular design, radar can be used to study avian ecology and behavior over a wide range of spatial and temporal scales (figure 5). Small portable radars operating locally can monitor moment-to-moment changes in a bird's location (Schmaljohann et al. 2008) over short distances (usually less than 5 km). These radars are frequently deployed near airports to help mitigate collisions of aircraft with birds and near wind farms as part of environmental
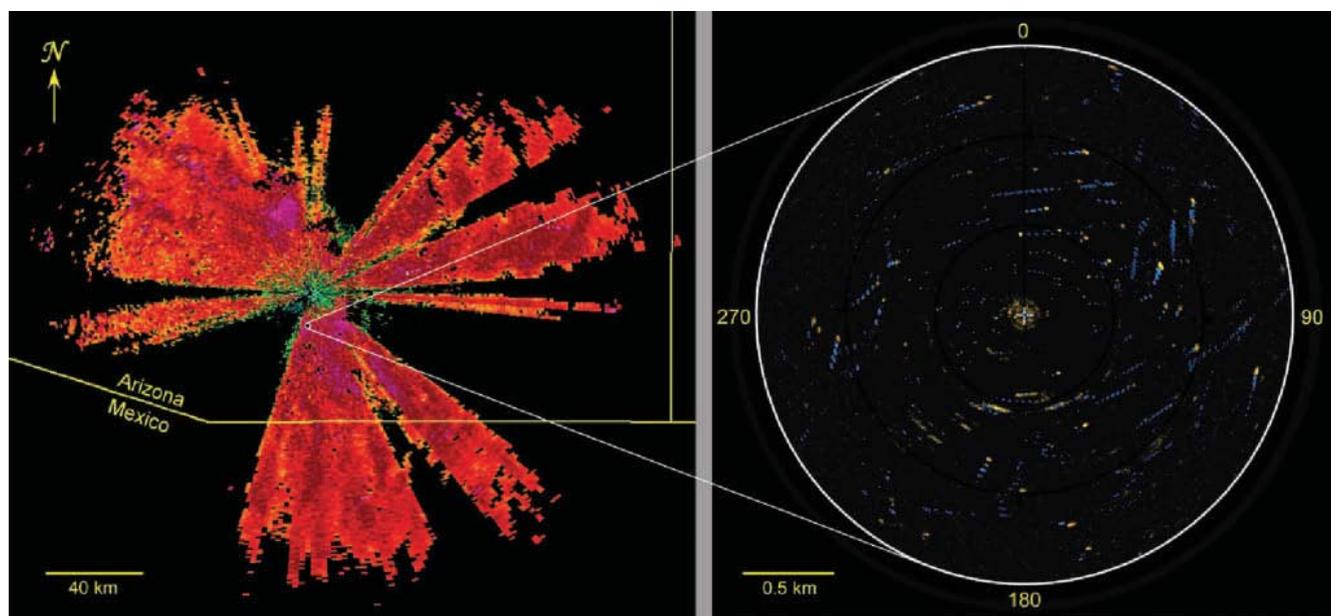
Figure 5. NEXRAD image of bird migration over southern Arizona on 18 April 2007 at 2243 Mountain Standard Time (left panel). The colors indicate logarithmically increasing numbers of birds from yellow to orange to red to pink. Topography partially or completely obstructs the radar's beam along some azimuths, which results in blank wedges in the pattern. A small area of NEXRAD coverage was simultaneously sampled using portable radar (expanded in the right panel). This snapshot occurred on the same day at 2248 Mountain Standard Time and shows at least 30 individual targets moving through the radar's field. The track of a target is represented by a train of blue dots (recent positions) capped by a yellow dot (current position). Target position updates every 2.5 seconds.

impact studies. In contrast, networks of long-range weather radars can be analyzed collectively to provide broad regional coverage, and this allows the structure of entire migratory systems to be studied at a continental scale.

The US National Weather Service maintains a network of weather surveillance Doppler radars (WSR-88D), collectively known as NEXRAD (for "Next-generation Radar"; Serafin and Wilson 2000). In Europe, the Operational Programme for the Exchange of Weather Radar Information employs a similar system, called the European Weather Radar Network (Dokter et al. 2011). These networks operate continuously and provide nearly complete spatial coverage across entire continents. In the United States, NEXRAD data are streamed over the Internet to a central processing facility and are freely available in near real time. Although they were built to collect meteorological data, radars within the NEXRAD system regularly detect the presence and movement of fly-ing animals as well (Gauthreaux et al. 2003). Together with proper complementary observations, systems like NEXRAD can provide an unprecedented means of observing birds, bats, and insects on both local and large scales.

Of course, radar has its limitations, and one should take care to match the research question to the strengths of a particular instrument. For example, compared with their portable cousins, NEXRAD radars provide a broader and more comprehensive view of the lower atmosphere and are more suited to providing data on birds en masse, rather than on specific individuals. If one is able to determine that the

bioscatter comes predominantly from a particular taxonomic group (e.g., songbirds or waterfowl), it is possible to estimate the density of the birds aloft (Diehl et al. 2003), along with their aggregate speed and direction, but not the flight paths of specific individuals. NEXRAD and similar systems are most valuable when observing, for example, the response of birds to weather systems, the locations and timing of major flyways, and how biomass is redistributed across the continent.

Despite some limitations, exploiting radar networks to study migration remains appealing for several reasons. One compelling advantage is that the radar hardware and infra-structure are already in place and are actively maintained. Furthermore, in the case of NEXRAD, the meteorological community has developed and freely distributed many soft-ware packages for accessing and visualizing both real-time and archived data. Nevertheless, one still requires a certain degree of training in order to properly utilize and interpret raw NEXRAD output. The weather community has con-fronted this issue by generating meteorological products from NEXRAD data, which allow forecasters to track severe weather, monitor rainfall rates, and issue tornado warnings without the need for excessive radar training. When creat-ing these data products, filtering algorithms are applied to remove bioscatter. However, by reprocessing the original radar data, which are archived at the National Climatic Data Center, radar-derived biological products could be pro-duced from bioscatter and made available to the public. The establishment of these products is still in development, but

a prototype Web server has been established to host these products as they become available (*http://soar.ou.edu*).

Numerous technological developments that are currently under way will further enhance our capability to study migration with radar. Hardware and software upgrades to many existing radar systems, including NEXRAD, will enable "dual-polarization" measures that will gather new kinds of data, such as body size and orientation, on birds, bats, and insects (Zrnić and Ryzhkov 1998, Doviak et al. 2000). The additional information provided by polarimetric radar will also aid in the ongoing development of algorithms for distinguishing between different kinds of biological and non-biological agents in the atmosphere. This type of automated target identification is a major challenge to the effective application of both portable and weather radars, but identification algorithms can greatly increase the range of biological questions that can be addressed, while decreasing the level of radar expertise needed to use the data. Another development is the design of a small radar beacon or transponder that can be detected and localized by weather radar—similar in concept if not in implementation to the harmonic radar used to track insects over short distances (see Chapman et al. 2011). A bird fitted with such a transponder would appear as a trackable "bright area" on the radar map. If these devices can be made small enough for birds to carry, we may have a revolutionary new method for monitoring small birds over long distances. Prototype beacons are currently being tested at the University of Oklahoma.

Information technology

Some of the tracking technologies described above have the potential to collect many thousands of locations for a given individual, making data management and analysis a new challenge in migration biology. New online databases offer tools not only for the management of tracking data but also for archiving and sharing (see supplementary table S2). These services are important for making the most of data that are often costly and difficult to obtain and for linking different studies to generate connectivity information for widespread species. The foremost online archive for tracking data is Movebank (*www.movebank.org*). Movebank is a free global repository for individually tracked animals that allows users to manage their data and share them either with the public or with only certain registered users. This new resource offers basic mapping and visualization, as well as integration with global weather data, and the administrators plan to incorporate additional analyses in future releases.

Existing and future information technologies will also enhance our interpretation of tracking data from weather radar networks. Several data portals provide free access to both extensive archived weather data as well as an abundance of free software for visualizing radar output (see table S2). Nevertheless, new tools specifically for the interpretation of biological data are needed. With the implementation of dual-polarized radar across the NEXRAD network, our ability to discern and classify animals in the aerosphere will be greatly enhanced, but we will need new software and new modeling approaches to exploit this potential (Shamoun-Baranes et al. 2010).

Modern cyberinfrastructure is also bringing new relevance to old monitoring techniques, such as bird banding and field observations. The Cornell Lab of Ornithology has recently founded the Avian Knowledge Network (AKN; see table S2) in an effort to consolidate observational records from a wide range of sources (e.g., banding stations, birding journals, point counts) and to make them available along with simple yet powerful analytical tools. Two features of the AKN are proving to be particularly valuable to bird-tracking studies. First, there is eBird (see table S1), a citizen-science initiative that exploits the recreational activities of an army of amateur bird watchers across the Americas (Sullivan et al. 2009). eBird provides a simple interface that allows birders to upload lists of recently sighted birds, and it stores these data in a publicly accessible archive. eBird also aggregates and organizes data, such that one can easily view phenomena such as the indigo bunting's (*Passerina cyanea*) northward migration along the Mississippi Valley in the spring (Marris 2010). As with radar-based tracking, eBird does not allow for tracking individual birds, but it does offer species-specific data that can provide a continental-scale perspective of long-distance migration movements. Another aspect of the AKN is the Landbird Monitoring Network of the Americas (LaMNA; see table S2), which represents a large-scale partnership directed at organizing diverse data sets resulting from bird banding operations and other data collection performed by professional scientists around the world.

Clearly, the most appealing aspects of these programs are their continental scope and data richness, and the potential for them to aid in migration studies is obvious. Still, some drawbacks are evident. With regard to eBird, it is quite likely that not all migratory birds are equal in the eyes of amateur birders. For a brightly colored species, such as the indigo bunting, eBird data are likely to be more extensive than for a less conspicuous species such as the Louisiana waterthrush (*Parkesia motacilla*). Indeed, the eBird archive shows roughly twice as many observations for the buntings than for the waterthrushes, but we do not know whether this difference reflects actual bird populations or observer bias. Although LaMNA may also suffer from detectability bias, banding data are generally derived from more standardized methods. Nevertheless, some may argue that LaMNA is too inclusive in its scope. In accepting such a wide array of data, it is difficult for LaMNA to maintain a uniform and integrated database. Therefore, data synthesis, which is the ultimate goal of this technology, may be limited by the diversity of the data sets.

Conclusions

Around 200 years ago, there was a serious debate about what happened to birds in the winter. Many people thought that birds hibernated, spending the winter in hollow trees or buried in the mud, but a few advanced the idea that the birds crossed vast distances to reach warmer climes in the

fall, only to return the following spring. In 1822, the first scientific evidence of long-distance migration presented itself in Germany in the form of a white stork impaled by an African spear. Although it was not intended as such, this spear was perhaps the first tracking device to aid in the study of migration.

Today, we are entering a new era in migration biology. Whereas information about migratory routes and connectivity was once derived from sparse and idiosyncratic band returns, inferences from biomarkers (e.g., genes and isotopes), or by cobbling together demographic data from separate populations, we now have an array of tools that allow us to visualize bird movements from the scale of the individual migration route to general migratory activity across a continent.

Of course, each of these tools has its strengths and weaknesses, and the choice of any tracking technology should be guided by the relevant research questions (reviewed in Robinson et al. 2010). For example, geologgers can help us generate information about the connectivity between breeding and wintering areas, which will in turn guide conservation efforts directed at preserving regional populations (Faaborg et al. 2010). In addition, accumulated satellite and GSM tracking data can reveal how migratory birds may serve as long-range disease vectors (Fair and Jankowski 2009, Takekawa et al. 2010, Altizer et al. 2011). Finally, weather radar data make evident a global "heartbeat," manifested by the seasonal movements of birds between breeding and wintering locations, and with the aid of long-term radar data sets now available, we can take the pulse of the planet in an age when climate change and land-use practices threaten numerous ecosystems (Cotton 2003, Carey 2009). As new communications technologies become available, we urge engineers and decisionmakers to consider how they might be used to enhance animal tracking. Only with new technology can we answer fundamental questions like the one that perplexed Gilbert White and address issues such as the impacts of climate change on biodiversity and disease dynamics that ultimately affect our own lives.

Acknowledgments

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