

CHAPTER 1

Animal Migration: A Context for Using New Techniques and Approaches

Keith A. Hobson* and D. Ryan Norris†

**Environment Canada*

†*Department of Integrative Biology, University of Guelph*

Contents

I. Introduction to Animal Migration	1
II. Migratory Populations, Connectivity, and Conservation	5
III. Scientific Tools Used to Study Migration	7
A. Extrinsic Markers	7
B. Transmitters, Radar, and Satellites	11
IV. Intrinsic Markers	12
A. Contaminants, Parasites, and Pathogens	13
B. Trace Elements	13
C. Stable Isotope Approaches	14
V. References	15

I. INTRODUCTION TO ANIMAL MIGRATION

The movement of organisms in space and time defines their interaction with their environments and, therefore, comprises a fundamental aspect of their ecology and evolutionary history. The degree to which organisms move also characterizes the range of resources they encounter, the array of hazards they experience from predators to hurricanes, and the degree to which they interact with other life forms. For animals, movement is very much a question of geospatial scale. While some species occupy a landscape of a few square meters for their entire lives or wander nomadically, others travel across thousands of kilometers in regular movements that constitute some of the most spectacular natural phenomena on the planet. These migrations are the movements that have captured the imagination of scientists and laypersons alike and leave us with a true sense of wonderment. Some key questions related to animal migratory movement include: How do these individuals know where they are going? How do they cope with the tremendous physical demands of travel? How do they adjust to unfamiliar or changing environments along the way to their destinations? How do they find their way back, often

to the precise location they left? Why do they move long distances in the first place? How is the abundance of populations influenced by where individuals go or where they are coming from?

Finding answers to these fundamental questions has proven to be an immense scientific challenge. A large part of this challenge has been the lack of tools available to scientists to infer or determine large- and small-scale animal movements. This volume explores recent developments in stable isotope methods that promise to contribute tremendously to the field of understanding animal movement in terrestrial ecosystems. However, before developing an understanding of those isotopic techniques, it is worthwhile exploring the scope of what we mean by migration.

The term *migration* often evokes images of spectacular seasonal movements of animals, especially birds, over vast distances. However, for thousands of years, where exactly birds went was one of the greatest natural mysteries of the world. In the *Iliad*, Homer believed that once cranes were done breeding in Greece, they flew to fight pigmies on the other end of the earth. In *On the History of Animals*, Aristotle famously hypothesized that [European] redstarts transformed themselves into Robins after the breeding season. Since redstarts leave Greece for Africa about the same time Robins arrive from their breeding sites further north, this seemed like a logical explanation. At the time, transmutation certainly seemed more plausible than birds traveling to other continents! Pliny the Elder (1855, 23–79 AD) was equally as inquisitive about seasonality in birds but a little more cautious. In Book X of his *Naturalis Historia*, he stated that “Up to the present time it has not been ascertained from what place the storks come, or whither they go when they leave us.”

The sense of awe and mystery is no less relevant today as we are witness to some spectacular migration phenomena by a variety of organisms (Figure 1.1). The Arctic Tern (*Sterna paradisaea*) migrates from breeding grounds in the Arctic to wintering grounds in the Antarctic, an annual round trip of a staggering 40,000 km (Hatch 2002), equivalent to 2 years of day-to-day driving by the average North American motorist. Salmon return by the millions to natal streams at the end of their lives after spending years moving thousands of kilometers in the open ocean (Quinn 2005). In the first year of their lives, eastern populations of Monarch Butterflies (*Danaus plexippus*) in North America travel to overwintering roosts in the transvolcanic mountain range of central Mexico, a trip that can be over 4000 km for an insect that weighs only 500 mg. For those of us living in temperate environments, the annual spring and autumn movements of billions of migratory birds, from warblers to waterfowl, likely provide the most familiar examples of migration. All these migrations really involve individuals moving between two worlds (Greenberg and Marra 2005).

Although these movements may be spectacular, much confusion still exists as to what exactly we mean by migration. Clearly, migration can include both *to-and-fro* and *one-way* movements. A *to-and-fro* or *round-trip* migration can be characterized by animals either returning on the same path or by individuals following a *loop* migration pattern. Various other patterns of movement have been described between origin and destination, especially for birds. For example, *leap-frog* migration involves individuals at the northern limits of their breeding range traveling the farthest south (in northern hemispheric animals) to most distant wintering grounds whereas those from more southern breeding regions migrate the least distance to more northern wintering grounds (e.g., Kelly et al. 2002). *Longitudinal* migration involves all individuals migrating the same approximate distance in a *chain* pattern or in *parallel* (Salomonsen 1955, Boulet and Norris 2006). Animal migration can be obligate whereby all members of a population move or facultative whereby resource availability may act to determine if migration occurs. *Partial migration* refers to a situation when only part of the population migrates. *Differential migration* describes those situations when migration patterns differ between sexes, age groups, or morphs within a population (Ketterson and Nolan 1976, Cristol et al. 1999).

One-way migration is probably a less common pattern of migration but is characteristic of many insects that move from the location they were produced to another location where they reproduce the next generation and die. That generation may then move on, repeating the process. In monarch butterflies, this occurs in a series of one-way steps involving multiple generations before a final cohort

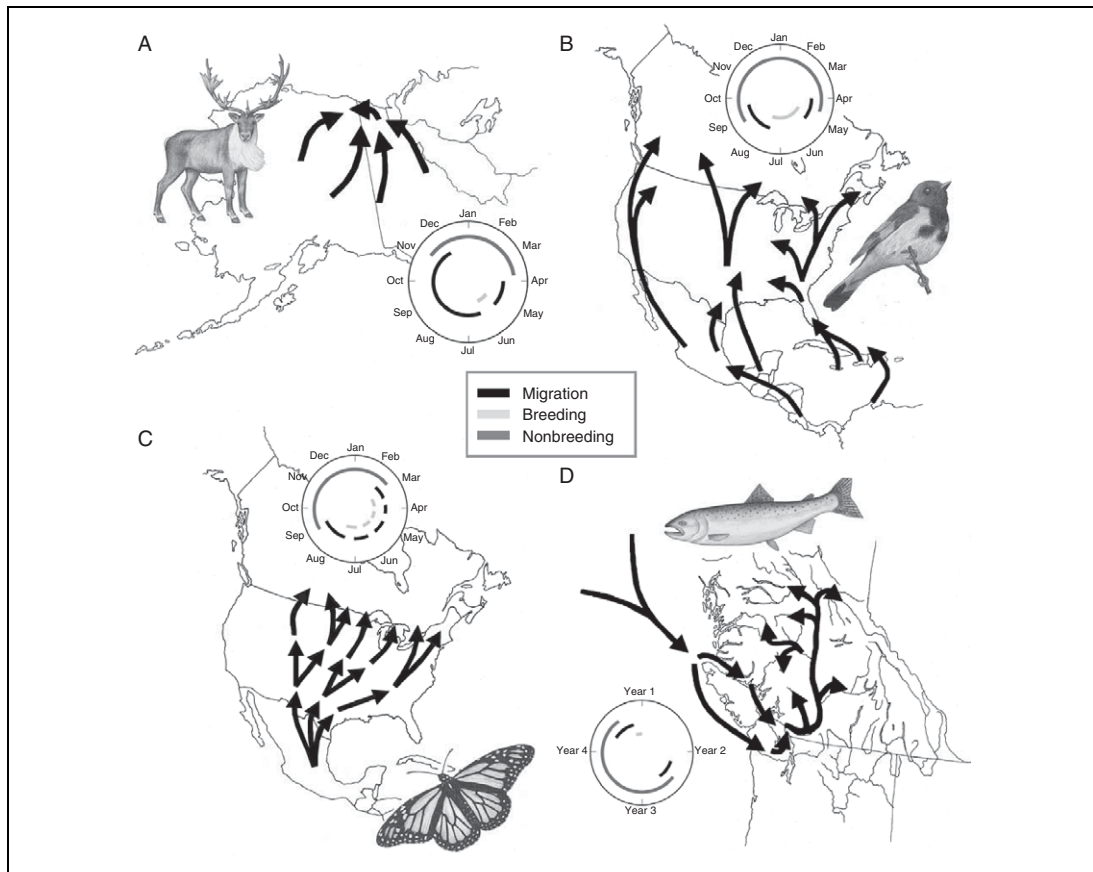


FIGURE 1.1 Examples of migration patterns in different taxa: (A) the Porcupine caribou herd (*Rangifer tarandus*), (B) songbirds (American redstart *Setophaga ruticilla*), (C) insects (Monarch butterfly *Danaus plexippus*), and (D) fish (Pacific salmon). Migratory pathways depicted by arrows are only generalizations.

returns to their starting point, overwinter roosts in the mountains of central Mexico. In other insects, such as the Black bean aphids (*Aphis fabae*), migration may involve a series of steps between host plants where individuals alternate between sexual and asexual reproduction (Cammell *et al.* 1989). Many salmon species also undertake spectacular migrations from the sea to freshwater rivers where they spawn and die. Although this is often considered one-way migration, it may be more accurately thought of as a “fatal round-trip migration” because offspring first have to migrate downriver where they spend several years at sea and then return to freshwater to spawn.

In mountainous habitats, animals may undergo *altitudinal* migrations where they seasonally track resource availability such as fruiting plants (Levey and Stiles 1992). These movements are more common in the tropics where frugivory is well developed and in more temperate areas of high relief. Although it may not seem like a form of migration, *nomadism*, where animals move in irregular patterns and breeding sites are established opportunistically where conditions are favorable, is a strategy employed by some animals. Several species of temperate forest seed-eating birds like crossbills, grosbeaks, and siskins are nomadic because of their reliance on cone crops or mast, which varies considerably in time and space (Newton 2006).

However, as Dingle (1996) noted, defining migration based solely on the outcomes (or patterns) such as to-and-fro, one-way, altitudinal, and nomadic movements can be somewhat problematic. For example, many animals also show to-and-fro or nomadic movements at a local scale within their *home*

range. Regular movements within a home range can involve commuting between resource patches such as hummingbirds moving between sources of nectar or between resource patches and reproductive sites as seen in wolves during the denning period and in many species of colonial nesting seabirds. These types of movements are not considered migration partly because they do not involve a persistent movement between two areas. By persistent, we mean that individuals undertaking the act of migration are rarely distracted during the period of movement (Dingle 1996). Contrast this with foragers inside a home range who will typically take advantage of resources as they occur opportunistically. Migration also requires special physiological and behavioral adaptations during the period of movement, whereas movements within a home range usually require no such changes.

Using these patterns to define migration also leads to confusion because it encompasses another important type of one-way movement that is distinctive from migration: dispersal. Dispersal is the movement between the place of birth and a new breeding area (natal dispersal) or the movement between breeding sites (breeding dispersal; Greenwood and Harvey 1982). In the case of many migratory animals who move to other areas after breeding, dispersal may also be considered as the movement between nonbreeding sites (nonbreeding dispersal). Thus, in the most general sense, dispersal can be thought of as the one-way movement between sites within a predefined season or period of time. Unlike migration, the act of dispersal neither does necessarily involve a persistent movement to a predefined geographical target nor does necessarily require behavioral and physiological adaptations.

The line between dispersal and migration in migratory species can oftentimes be quite blurred. For example, consider an individual born at one location that migrates to a nonbreeding area and then migrates back to a different breeding site. In this case, the individual has both migrated (between breeding and nonbreeding sites) and dispersed (moved from one breeding site to another). Note that both migration and dispersal can be estimated without knowledge of the other process. For example, one could determine where an animal bred the previous year without knowledge of where it migrated to the previous season. Similarly, one may be able to determine where an individual migrated from the previous season without knowledge of where it bred the previous year. Knowledge of both processes is important for understanding the factors that influence individual fitness and population dynamics.

So, how do we define migration? A key underlying concept is that migration is typically in response to seasonal changes in resource abundance. As noted by Dingle and Drake (2007), migration can be considered an adaptation specific to arenas in which changes in habitat quality in different regions occur asynchronously so that movement allows a succession of temporary resources to be exploited as they arise. In this sense, migration involves escape and colonization. In their holistic view of migration, Dingle and coworkers see the arena as the environment to which migrants are adapted and the migration syndrome is the suite of traits enabling migratory activity that involves both locomotory capabilities and a set of responses to environmental cues that schedule and steer the locomotory activity. In this respect, migratory movements can be differentiated from movements within a home range or dispersal. Their conceptual model also includes a genetic complex that underlies the syndrome and a population trajectory comprising the route followed by the migrants, the timing of travel and stops along it, and the periods and locations corresponding to breeding and other key life-history events. The migration system involves a species' specific migration syndrome that determines how the animal responds to external cues so that preemptive movements can occur prior to resource collapse. A fascinating area of study involves understanding those physiological adaptations to migration, including the incorporation of reproduction and other tasks (Ramenofsky and Wingfield 2007) and the underlying genetic processes that result in selection for specific migratory traits (Pulido 2007, Roff and Fairbairn 2007).

As Dingle (1996) points out, the definition of migration must be based on the behavioral and physiological processes involved with the movement rather than the spatial pattern or outcome. Thus, we consider migration as the movement away from the home range that does not cease (at least not initially when suitable resources are encountered) which requires a set of behavioral and physiological adaptations for sustained movement that are unique from day-to-day adaptations related to self-maintenance and breeding.

II. MIGRATORY POPULATIONS, CONNECTIVITY, AND CONSERVATION

Although selection for adaptive traits related to migration is thought to occur at the individual level, migration systems and patterns are more often described at the population level, typically as the migration of populations or subpopulations within a species. We usually deal with population units when engaging conservation efforts and the conservation of populations that move over large distances presents considerable challenges (Webster *et al.* 2002, Marra *et al.* 2006). Populations of animals might be well protected and managed at one location, but then suffer no protection once they leave that area. For long-distance migrants, their travels may take them to new geopolitical jurisdictions where conservation measures are absent or inadequate. It makes little sense to expect migratory populations to respond positively to local conservation measures if key aspects of individual fitness or overall population health are being influenced at another location.

The problem of conserving species whose life-cycles cross geopolitical borders has become a profound issue in the twenty-first century as habitats everywhere are being reduced in size or quality, and migrants are forced to move among a myriad of patches, each with its own level of quality, safety, and prospects for future existence (Robinson *et al.* 1995, Moore *et al.* 2005). In this sense, migratory organisms are best considered to be made up of series of populations (that may or may not mix between different periods of the year) rather than as a single species *per se*. For some animals, populations breeding in one area may follow similar migration routes and winter in the same general wintering region. In this case, we would consider the subpopulations to show *strong connectivity*. Other breeding populations may disperse widely on the wintering grounds (or vice versa), which can be considered a case of *weak connectivity*.

The concept of migratory connectivity is important to conservation. Many forms of connectivity are possible (Webster and Marra 2005, Boulet and Norris 2006) ranging from the extreme cases where, for example, individuals of breeding populations show high philopatry to the same wintering location. Among birds, the Kirtland's Warbler (*Dendroica kirtlandii*) is a good example because the small breeding population in Michigan winters exclusively in the Bahamas. Weak connectivity may involve individuals from many breeding populations mixing among many wintering populations or vice versa. Quantifying patterns of connectivity can be difficult. One approach is to compare observed patterns of connectivity against the null hypothesis of complete mixing based on relative abundance (Norris *et al.* 2006). For example, let us say that a wintering population is sampled to estimate the geographic location of their breeding site. Suppose there are three potential breeding sites (A, B, and C) with the relative abundance of 0.6, 0.3, and 0.1, respectively. The null expectation for a sample of wintering birds would, therefore, be equal to the relative abundance of the breeding populations. Deviations from this expectation would indicate stronger than expected connectivity. The problem with this approach is that estimates of relative abundance are rarely available throughout a species entire range (all potential breeding sites).

Populations with strong connectivity are hypothesized to be those that are most vulnerable to declines because they have little chance to be "rescued" by peripherally connected populations (Marra *et al.* 2006). On the other hand, it is the strongly connected populations that may benefit the most from conservation efforts because the connections between two or more areas are well established. Although populations of weakly connected individuals may be inherently "safer," in the sense that risk is spread among more locations, these populations will understandably be harder to manage unless measures are enacted over large regions that encompass a significant percentage of the subpopulation of interest. It may also be more difficult to identify the causes of population declines in subpopulations that are weakly connected. For example, when migratory populations are mixed between two periods, habitat loss in one subpopulation may produce synchronous declines in subpopulations in the following season (Marra *et al.* 2006).

Knowledge of migratory connectivity is also important for being able to predict how conservation measures in one season will influence populations the following season. For example, [Martin *et al.* \(2007\)](#) demonstrated that the protection of nonbreeding habitat for American redstarts (*Setophaga ruticilla*) based on rate of habitat loss, density, and land cost resulted in the almost complete extinction of one breeding region. This was because the criteria for deciding where and when to conserve nonbreeding habitat did not consider where individuals were spending the remainder of the annual cycle. Consideration of how populations are connected can, therefore, result in radically different decisions on how to allocate resources for conserving species.

In many ways, most migratory animals have evolved to maintain ambient conditions as constant as possible throughout the annual cycle. This contrasts with resident species in temperate areas that must adjust seasonally to extreme changes in weather and foraging opportunities. As such, it is debatable whether or not migrants are inherently more adaptable or plastic in their behaviors compared to nonmigrants. This issue is particularly interesting in view of global anthropogenic and natural environmental, landscape, and climatic changes that have occurred over decadal and millennium scales and will continue into the future ([Crick 2004](#), [Møller *et al.* 2004](#)). For migratory birds, it is not clear whether they will be able to quickly adapt to anthropogenic changes wrought on a decadal timescale ([Møller *et al.* 2004](#)).

Timing of breeding has important implications for avian productivity and is one of the traits most noticeably affected by spring weather conditions ([Dunn and Winkler 1999](#), [Winkler *et al.* 2002](#), [Dunn 2004](#)). Birds that nest earlier generally produce more offspring that are ultimately recruited into breeding populations ([Perrins 1970](#), [Dunn 2004](#)). It remains uncertain whether migratory birds and other animals will be able to continue to synchronize the timing of their breeding with optimal conditions for reproduction on breeding areas in light of changes in climate and land use ([Visser *et al.* 1998, 2004](#), [Both and Visser 2001](#), [Sanz *et al.* 2003](#)).

In their long-distance travels that cross international borders, migratory animals can also act as vectors of parasites and pathogens. There are a number of ornithophilic mosquitoes that can infect migratory birds that in turn act as introductory or amplifying hosts ([Rappole *et al.* 2000](#), [Reed *et al.* 2003](#)). Recent interest in the spread of avian influenza viruses around the globe has increased the interest in determining the migratory origins of infected and noninfected wild birds ([Liu *et al.* 2005](#)). This level of interest will only increase as the global climate and the distributions of suitable habitats available to these pathogens change over time.

Effective management of species also requires identifying where populations are most productive. We are all familiar with field guides that show the absolute spatial ranges occupied by a given species, but where within that vast space are the most young being produced and recruited into the autumn migratory population and where are individuals experiencing the highest survival rates during the nonbreeding period? Understanding where hot spots of productivity and survivorship occur helps us protect those places and better understand factors that may be limiting populations. Nor are species necessarily more productive where they are most abundant, and numerous examples exist of how animals can be lured into ecological traps where they suffer reduced success. For migratory game birds, understanding how zones of productivity relate to protected areas and the timing of harvest is particularly crucial to their conservation.

For many years, our understanding of the ecology of migrant organisms was understandably influenced by their activities during the breeding season in locations where they were accessible to scientists working in the temperate regions. Such interest was also driven by an assumption that decisions made by individual animals related to breeding were of paramount importance to an individual's fitness. Aspects of breeding success related to habitat choice, mate choice, timing of breeding, and the quality of individuals were topics that were considered largely as they played out on the breeding grounds, with little regard to events that preceded and followed them on the wintering grounds and during migration. This situation changed in the 1980s when waterfowl researchers began to discover that female body condition upon arrival on the breeding grounds in spring was linked to

conditions she experienced in winter, and that these could have profound influence on the number of young recruited into the autumn population (Heitmeyer and Fredrickson 1981, Kaminski and Gleusing 1987).

In the late 1990s, it has become more widely accepted that events occurring outside the breeding area can profoundly affect the fitness of migratory individuals. Much of this recent interest has been generated from the work of Marra *et al.* (1998) who, using stable isotopes, first demonstrated in American redstarts a clear link between spring arrival times of males and the quality of the habitat they occupied in winter. The quality of a habitat where an animal winters will determine the level and speed with which the necessary body condition for migration can be reached, and so can determine when and in what condition that individual arrives on the breeding grounds. Several studies of birds have shown that earlier arriving birds can obtain better territories, initiate clutches sooner, and generally fledge more young than those arriving later (*e.g.*, Gill *et al.* 2001, Bêty *et al.* 2003, Norris *et al.* 2004). How costs associated with reproduction might influence an individual's ability to compete during the nonbreeding season remains a mystery. Nonetheless, seasonal interactions between the wintering grounds and the breeding grounds, as well as during migration itself, should ultimately play a large role in determining lifetime fitness and population abundance (Norris and Marra 2007).

Establishing details of migratory programs in animals is fundamental to understanding key aspects of their evolution, life history, and conservation. The field has witnessed a renaissance in recent years primarily because the development of new analytical techniques has provided some true breakthroughs. There is also a more urgent sense that we need to more quickly understand key migratory linkages for animal populations in order to help conserve them in a rapidly changing world. It is in this spirit that we developed this volume on stable isotope techniques because that approach has and will continue to contribute immensely to the study of animal migration. We also recognize that, as with all techniques and approaches, there is a real need to provide a firm foundation for practitioners and to point to ways in which the field might best progress.

III. SCIENTIFIC TOOLS USED TO STUDY MIGRATION

A. Extrinsic Markers

Tracking migratory terrestrial animals has involved numerous techniques over the years (Table 1.1). Until very recently, all approaches involved the use of extrinsic markers applied to individuals with the hope of relocating those same individual elsewhere, or on the use of recognized phenotypic or morphological traits that showed known geographic variation. For birds, there is a rich literature on geographic variation in plumage and morphology and these traits have been used to describe migratory connectivity. A good example is the Yellow-rumped Warbler (*Dendroica coronata*) that shows plumage variation between eastern (*coronata*) and western (*audubon*) races in North America and that also segregates largely on the wintering grounds. Similarly, the Swainson's thrush (*Catharus ustulatus*) occurs as a reddish backed phenotype on the Pacific coast of North America and a more common olive-backed form elsewhere. Birds captured during migration can readily be placed into these types without the need for mark-recapture techniques. Most current field guides provide numerous examples of geographic variation in plumages (Sibley 2001). An excellent example of how plumage and morphometrics have been used to describe migration patterns in Nearctic–Neotropical migrant birds that moved through Mexico was that of Ramos and Warner (1980) and Ramos (1983). However, typically the geographic resolution provided by this approach is both poor and highly variable among taxonomic groups. For example, as noted by Boulet and Norris (2006), within the 50 species of migratory wood warblers of the New World, 65% are monotypic, 30% include 2–4 subspecies, and only 6% include 5 or more subspecies.

TABLE 1.1 Summary of various techniques used to track migration in animals

Technique	Advantages	Disadvantages	References
Extrinsic	<ol style="list-style-type: none"> 1. can apply to a broad range of animals, 2. high spatial resolution. 	<ol style="list-style-type: none"> 1. requires initial capture and then recapture, 2. biased toward initial capture population 	Ramos (1983), Ramos and Warner (1980), Bell (1997), Boulet and Norris (2006)
Phenotypic variation (<i>e.g.</i> , morphology, plumage)	<ol style="list-style-type: none"> 1. inexpensive, 2. can be applied to historical specimens with high degree of confidence. 	<ol style="list-style-type: none"> 1. low resolution, 2. not applicable to all species, 	
Banding/marking	<ol style="list-style-type: none"> 1. inexpensive, 2. provides exact information on start and end of movements. 	<ol style="list-style-type: none"> 3. provides estimate of natal origin only 1. many species have low recovery rates (<0.5%), 2. can take many years to get adequate data, 3. still only a small number of major banding stations across globe, 4. both marking and recovery (start and end points) are biased toward locations of major banding stations. 	Brewer <i>et al.</i> (2000), Bairlein (2001), Berthold (2001)
Radio transmitters	<ol style="list-style-type: none"> 1. produces precise locations (relative to extrinsic markers through triangulation, 2. can obtain precise trajectory if within range of transmission. 	<ol style="list-style-type: none"> 1. low range 2. expensive relative to banding or morphological methods, 3. Some evidence suggests transmitters can have adverse effect on behavior 	Vega-Rivera <i>et al.</i> (1998), Cochran <i>et al.</i> (2004)
Satellite transmitters	<ol style="list-style-type: none"> 1. precise animal trajectory. 	<ol style="list-style-type: none"> 1. expensive (severely constrains sample size), 2. constrained to large animals only (~300 g), 3. some evidence suggests that transmitters can have adverse effect on behavior. 	Britten <i>et al.</i> (1999), Hays <i>et al.</i> (2001), Berthold <i>et al.</i> (2002)
ICARUS Project	<ol style="list-style-type: none"> 1. small and light transmitters allow many types of species to be tracked, <p>similar to satellite tags, can track individuals over large distances (global),</p>	<ol style="list-style-type: none"> 1. huge start-up investment, 2. not yet proven technology, 	Wikelski <i>et al.</i> (2007)

passive radar	<ul style="list-style-type: none"> 3. inexpensive following start-up investment. 1. coverage over large geographic area, 2. inexpensive, 	<ul style="list-style-type: none"> 3. like above, some evidence suggests that transmitters can have adverse effect on behavior. 1. coverage only from existing stations or portable instruments, 2. poor ability to determine species-and individual-specific movements 	Bruderer (1997), Gauthreaux and Belser (2003)
Transponders	<ul style="list-style-type: none"> 3. individuals do not have to be captured. 1. small transponder size. 	<ul style="list-style-type: none"> 1. Requires external (radar/microwave) activation, 2. low range, 3. coverage only from existing stations or portable instruments. 	Riley <i>et al.</i> (1996)
Archival geolocation tags	<ul style="list-style-type: none"> 1. produces an animal trajectory; interval between recorded locations can be customized, 2. light weight (as low as 1.5 g), 3. inexpensive relative to satellite tags (but more expensive than radio transmitters) 	<ul style="list-style-type: none"> 1. individuals must be recaptured to download data, 2. accuracy relative to satellite tags still low (~200 km) 	Shaffer <i>et al.</i> (2005, 2006)
Intrinsic	<ul style="list-style-type: none"> because only requires one capture, it is: 1. not biased to initial capture population, 2. less labor intensive than most extrinsic methods. 	<ul style="list-style-type: none"> 1. biased to final captured population (can be overcome by comprehensive sampling coverage), 2. typically lower resolution than extrinsic markers. 	Hobson (1999), Webster <i>et al.</i> (2002), Rubenstein and Hobson (2004)
Contaminants	<ul style="list-style-type: none"> 1. potentially high spatial resolution (e.g., Mirex). 	<ul style="list-style-type: none"> 1. lack of a priori maps of distribution and relative abundance, 2. distribution of containments may be vary predictably over geographic areas, 3. potential transport of contaminants may dampen or provide unreliable geographic signal. 	Ochoas-Acuna <i>et al.</i> (2002), Braune and Simon (2003)
Parasites Genetics	<ul style="list-style-type: none"> 1. several markers possible, 	<ul style="list-style-type: none"> 1. species specific, 	Fallon <i>et al.</i> 2006 Kelly <i>et al.</i> (2005), Smith <i>et al.</i> (2005), Boulet <i>et al.</i> (2006)

(continued)

Table 1.1 (continued)

Technique	Advantages	Disadvantages	References
Trace elements	<p>2. east vs west resolution of migratory fauna in North America.</p> <p>1. simultaneous measurement of a large number of elements, 2. potentially high spatial resolution.</p>	<p>2. typically low resolution,</p> <p>3. provides estimate of natal origin only.</p> <p>1. lack of a priori maps of distribution and relative abundance, 2. expensive, 3. requires more sample tissue than either isotopes or genetic markers, 4. requires sampling of tissue that is metabolically inert after growth, 5. spatial resolution could be too high (<i>i.e.</i>, requires sampling of all possible populations), 6. evidence that some elements may be integrated into metabolically inactive tissues after growth is complete.</p>	<p>Parrish <i>et al.</i> (1983), Kelsall (1984), Szep <i>et al.</i> (2003), Norris <i>et al.</i> (2007)</p>
Stable isotopes	<p>1. inexpensive,</p> <p>2. not species or taxon specific,</p> <p>3. multiple isotopes can be combined to increase spatial resolution.</p>	<p>1. often low resolution,</p> <p>2. lack of isotopic basemaps for several elements, 3. ideal tissue is metabolically inactive after growth, 4. for metabolically active tissue, turnover rate of elements unknown for many tissues/species, 5. Animal physiology may influence dD values of body water and so complicate interpretations.</p>	<p>Chamberlain <i>et al.</i> (1997), Hobson and Wassenaar (1997), Hobson (1999, 2005), Norris <i>et al.</i> (2006), this volume</p>

By far the most widespread approach to tracking migrant animals is through the application of passive extrinsic markers. For birds, these have overwhelmingly involved leg bands or rings carrying a unique number combination and some instruction on where to report the band if it is recovered. Other markers such as patagial tags, numbered neck collars, streamers, or color dyes have also been used. Insects have proven to be more of a challenge due to their small size, but numbered labels have been successfully affixed to the wings of butterflies and later recovered (www.monarchwatch.org). In the relatively short historical period (*i.e.*, 100 year) of banding birds, many millions of individuals have been individually tagged. For a number of species with small global populations and restricted ranges, some very impressive recovery rates have been achieved (*e.g.*, Owen and Black 1989) and some key insights into migratory connectivity established (Gill *et al.* 2001). However, for the vast majority of species, extremely low recovery rates (*i.e.*, <0.01%) are the norm (Hobson 2003).

B. Transmitters, Radar, and Satellites

Active extrinsic markers are those that send out signals that can be intercepted with a suitable receiver device. Advances in transmitter technology have allowed the placement of devices on migratory animals. If a receiver is within range of the transmitter, then the location of the animal can be inferred either by tracking down the individual or by triangulation with more than one receiver. Radio-frequency transmitters can be made small enough (0.5 g or lower, see below) to place on small passerines and bats. However, with miniaturization comes a loss of both range and battery life so that optimally, these devices provide location information up to a few kilometers. Nonetheless, adventurous researchers have attempted to follow migrating birds, bats, and even dragonflies equipped with transmitters over at least portions of their flight paths (Wikelski *et al.* 2003, Cochran *et al.* 2004, Holland *et al.* 2006). Using a combination of aerial and ground tracking receivers, Wikelski *et al.* (2006) followed the southward migration of dragonflies (Common green darner *Anax junius*) equipped with 300 mg radio transmitters. Presumably, placement of automatic receivers, such as one that is already in place on Barro Colorado Island, Republic of Panama (M. Wikelski, personal communication), could monitor the presence of an individual at a few key locations like stopovers or areas where migrants are concentrated, but such an approach is still a bit like trying to locate a needle in a haystack. Cell phone technology has also provided new possibilities for tracking animals but the miniaturization and development required for animal tracking is a hurdle. As well, cell phone network coverage is limited at a global scale and locational accuracy is low (Stokely 2005). A final concern is that the fastening of markers or transmitters may alter flight or movement behavior.

Radar technology has made great contributions to our understanding of migration because this provides information of flying animal movements over considerable distance (Gauthreaux and Belser 2003). However, like automated receivers, radar installations are often fixed, and mobile radar systems are generally impractical to follow animal movements over migratory distances. Crossband transponders placed on migratory organisms can be used to elicit a detectable radio frequency signal after the transponder is intercepted by radar. The transponder is dormant until such an event and so can last for a much longer period than conventional “always transmitting” radio frequency tags. However, such *active* radar systems face a number of limitations, again related to size and weight of instrumentation and the need to intercept the organism of interest within range of the radar system (see www.earthspan.org).

Satellite transmitters have provided a major advance in methods to track migratory animals because they provide extremely accurate positions of individuals remotely. Precise trajectories of individuals are possible over vast portions of the globe that have suitable satellite coverage. Satellite tracking systems such as ARGOS (www.argosinc.com) have been placed on different satellites from the US National Oceanic and Atmospheric Administration, The Japanese Space Agency, and the European Meteorological Satellite Organization. The ARGOS system collects data from platform terminal transmitters and

delivers telemetry data back to the user. Unlike other extrinsic techniques, this approach does not require the physical capture of individuals once they are marked (although many researchers attempt this in order to recover the expensive transmitters). One of the most spectacular examples of this approach was provided by [Jouventin and Weimerskirch \(1990\)](#) who tracked Wandering albatrosses (*Diomedea exulans*) on foraging flights up to 15,000 km. Future prospects for this technology are encouraging and there is strong interest in diminishing the size of transmitters and batteries so that smaller species can be monitored. Currently, the smallest satellite tags available are about 9.5 g and potentially could be used on 240 g animals (using the <5% body weight rule, Murray and Fuller 2000). Unfortunately, this still excludes about 81% of the world's birds and 68% of the mammals and, of course, all migratory insects ([Wikelski et al. 2007](#)).

The use of satellites may potentially provide a major breakthrough in tracking migratory animals down to the size of large insects. [Wikelski et al. \(2007\)](#) have proposed that a new satellite equipped with radio receivers could track radio tags with radiated power as low as 1 mW with an accuracy of a few kilometers under favorable conditions. This power can be achieved from existing radio frequency tags as small as <1 g. This approach is similar to solutions derived by space researchers who need to detect very weak signals from distant galaxies and so the technology exists to modify the solution to detecting weak radio signals from earth amidst a background of much stronger radio frequency noise. A group known as International Cooperation for Animal Research Using Space (ICARUS, www.icarusinitiative.org/solutions) is promoting this idea as a means of tracking small animals around the globe. They estimate that it will take about US\$50–100 million in order to build and launch a satellite.

A relative new application for tracking migratory animals is the use of archival geolocation tags ([Shaffer et al. 2005, 2006](#)). These tags estimate longitude and latitude based on light levels and sea-surface temperatures, and long-distance movement data have now been reported on shearwaters ([Shaffer et al. 2005](#)) and albatross ([Shaffer et al. 2006](#)) with several more species currently being tested. The advantage of these tags is that they are significantly lighter than satellite transmitters (now 1.5–3 g). However, the disadvantage is that their accuracy, using both combined light levels and sea-surface temperatures, is only ± 200 km that restricts application of these tags to questions pertaining only to large-scale movements.

With the exception of satellite transmitters, all extrinsic markers require that the individual be recaptured, resighted, or at least move within detection distance at a later time. The probability of this recapture will clearly be the product of a number of individual probabilities related to the number of observers, the likelihood of an observer reporting the information, the regions and habitats used by the animal, and so on. As we have seen, combining these probabilities can result in vanishingly small chances of obtaining information on any given individual.

Apart from the burden of recovering a marked individual, the use of passive extrinsic markers suffers another fundamental flaw—they provide information only on the movement of marked individuals. The possibility of extrapolating the findings based on a small marked cohort to the population or species level depends on how representative the marked individuals are. Our confidence in this approach increases with the number of independent recaptures and some band recovery data show unequivocal patterns that are clearly representative of populations. A single band recovery or satellite track while interesting and ultimately useful may tell us very little about what populations are doing.

IV. INTRINSIC MARKERS

The primary advantage of intrinsic markers is that initial marking of individuals is not necessary and that every capture provides information on origin. In this sense, every capture becomes a recapture. The sampling scheme is biased then, only by the limitations of where animals are ultimately

located and this typically represents a much less serious form of bias compared to where individuals can be marked initially using extrinsic markers.

A. Contaminants, Parasites, and Pathogens

There are several forms of potential intrinsic markers that can be used to infer origins of migratory animals. If the spatial distribution of a suite of contaminants were known, then presumably the occurrence of contaminants in animals could provide some information of the past distribution of the animals being sampled. Although this approach has not yet been used to any significant degree, there is some interesting potential here. For example, Braune and Simon (2003) noted that in contrast to Thick-billed Murres (*Uria lomvia*) and Black-legged Kittiwakes (*Rissa tridactyla*), the pattern and concentration of dioxin/furan congeners as well as the ratio of total PBDEs to HBCD (hexabromocyclododecane) in Northern Fulmars (*Fulmarus glacialis*) breeding in the Canadian high Arctic was suggestive of them wintering in the northeast Atlantic. In the Great Lakes region of North America, mirex could be used as a marker to distinguish among those waterbirds breeding and wintering in different regions because the upper lakes have much lower concentrations of this contaminant than the lower lakes. The ratio of DDE to PCB can also be used to illustrate which birds have likely overwintered in agricultural areas of South/Central America versus coastal areas (B. Braune, unpublished data). Brominated flame retardants are another material that occurs in greater concentrations in food webs used by animals exposed to European air masses than those exposed to North American air masses (de Wit 2002). Finally, methyl mercury and other heavy metals are another potential marker in migratory animals because exposure to these varies considerably throughout the world (Harjo and Uuksulainen 1993, Janssens *et al.* 2002, Ochoas-Acuna *et al.* 2002).

Similar to contaminants, parasite and pathogen exposure experienced by migratory animals varies geographically and there is interest in using these markers to examine movements of assayed individuals (Ricklefs *et al.* 2005). Very little research has been conducted on these sorts of tools to assist with deciphering animal movements, perhaps because we have little information to begin with on the spatial distributions of the potential markers themselves. On the other hand, the use of genetics has generated more interest because it is possible to assay and describe genetic variation across breeding populations and then to use this information to assign a probability that a given individual came from a given (known) subpopulation (Smith *et al.* 2005). The identification of population structure using genetic markers has included the use of allozymes, mitochondrial DNA sequences, and DNA fragment analyses such as microsatellites and amplified fragment length polymorphism. These markers can yield different scales of population structure because they evolve at different rates. In North America, genetic markers have been particularly useful in differentiating between eastern and western breeding origins of wintering Neotropical migrant songbirds (Smith *et al.* 2005, Boulet *et al.* 2006), reflecting patterns of rapid demographic expansions following glaciation events on that continent. The combination of marker techniques that can provide information on north-south origins in North America would clearly augment the resolution of genetic approaches. Genetic analyses also hold great potential for developing parasite markers in migrant organisms because PCR-based assays of blood parasites can now identify pathogens to species and haplotype (Ricklefs *et al.* 2005).

B. Trace Elements

Trace elements are another set of intrinsic markers that can potentially be used to track individual movements over both small and large geographic distances. Similar to stable isotopes, the idea with trace elements is that individuals acquire distinctive chemical profiles at one geographic location and then carry that profile with them to another area where they can be sampled to estimate their

geographic origin. In the past, one of the limitations of using trace elements was the amount of sample required for analysis. However, the use of inductively coupled plasma mass spectrometers has allowed smaller quantities of samples (3 mg; T. K. Kyser, personal communication; [Donavan et al. 2006](#), [Norris et al. 2007](#)) to be measured with relatively high precision. This technological advance has allowed researchers to focus on nondestructive tissues, such as metabolically inactive keratin, that are grown during specific periods of the migratory cycle. Trace element profiles have been used to infer whether individuals sampled in the same breeding population originate from different places the previous winter ([Szep et al. 2003](#)).

However, because we have little idea of how trace elements vary over the landscape, the ability of this technique to estimate the precise origin of individuals seems, at the moment, limited. To determine how trace elements vary across the landscape, [Norris et al. \(2007\)](#) measured 42 trace elements in feathers of western sandpipers (*Calidris mauri*) at 5 different locations on their tropical wintering grounds. Feathers were grown during the winter periods and were, therefore, assumed to provide a signature of known-origin. Elemental profiles successfully distinguished between birds wintering at all five locations. However, two locations were less than 3 km apart suggesting that trace elements are likely very specific to the location or origin in which they were sampled. Trace element approaches are probably best suited to species that are aggregated over only a few breeding or wintering sites so the majority of populations can be sampled over the entire range ([Donavan et al. 2006](#)). Studies several years ago also show that some trace elements in feathers may be acquired after growth ([Bortolotti and Barlow 1988](#), [Bortolotti et al. 1988](#)), implying that this may not be a reliable approach for tracking long-distance movements. Further studies are needed to test the generality of these results before trace elements can be widely used as a marker of geographic location.

C. Stable Isotope Approaches

The intent of this volume is to provide the reader with a comprehensive background needed to understand the application of stable isotope tools to the study of animal migration. This is a new and exciting field and we are seeing a rapid increase in the number of researchers using this approach. However, animal ecologists have really only recently become aware of using stable isotope measurements in ecological studies in general. The world of stable isotopes is a multidisciplinary one that has a very rich history involving physics, earth sciences, biogeochemistry, animal and plant physiology, and even anthropology and archaeology. The 1988 publication of the book *Stable Isotopes in Ecological Research* edited by [Rundel et al. \(1988\)](#) marked a significant pivot point that informed ecologists of the immense potential of stable isotope measurements in natural ecosystems. This was quickly followed up with *Stable Isotopes in Ecology and Environmental Science* edited by [Lajtha and Michener \(1994\)](#), which is now updated to [Michener and Lajtha \(2007\)](#). Most recently, [Fry \(2006\)](#) has produced a useful text that provides some of the necessary background to understanding fundamental concepts in stable isotope ecology and [Karasov and Martínez del Río \(2007\)](#) provide a very useful overview of key linkages between animal physiology and isotopic ecology.

In [Chapter 2](#), the essential background required to understand the behavior of stable isotopes in nature, their measurement, and the fundamentals of mass spectrometry is provided. This chapter will provide the reader with a good starting point for stable isotope applications as well as the field of tracking migration. [Chapter 3](#) introduces fundamental concepts and principles underlying isotopic tracking of migration and provides a perspective on the history of this approach in terrestrial systems. Key examples are used to illustrate specific concepts but the reader is also provided with a detailed summary of most work to date. Many examples will include birds. In part, this reflects the fact that avian biologists have been quick to apply isotopic techniques to a number of facets of bird ecology. Birds are also well studied relative to other taxa and provide some of the best subjects for the study of migration in vertebrates.

In Chapter 4, isotopic patterns across landscapes are reviewed that can be used to infer animal origins. These “isoscapes” provide the fundamental templates upon which migration is played out. This is a current area of exciting research involving remote sensing and Geographic Information Systems to portray expected spatial patterns. In Chapter 5, the numerous ways in which isotopic data can be analyzed to infer the origin of individuals are reviewed and analyzed. Because methods of assigning individuals have vastly improved over the last few years, suggestions for researchers embarking on designing studies to track migratory animals using stable isotopes are also provided. Finally, Chapter 6 combines the thoughts of all authors and others to help establish the way forward.

V. REFERENCES

- Bairlein, F. 2001. Results of bird ringing in the study of migration routes. *Ardea* **89**:7–19.
- Bell, C. P. 1997. Leap-frog migration in the Fox Sparrow: Minimizing the cost of spring migration. *Condor* **99**:470–477.
- Berthold, P. 2001. *Bird Migration. A General Survey*. Oxford University Press, Oxford.
- Berthold, P., W. V. D. Bosch, Z. Zakubiec, C. Kaatz, M. Kaatz, and U. Querner. 2002. Long-term satellite tracking sheds light upon variable migration strategies of White Storks (*Ciconia ciconia*). *Journal of Ornithology* **143**:498–493.
- Bêty, J., G. Gauthier, and J.-F. Giroux. 2003. Body condition, migration and timing of reproduction in Snow Geese: A test of the condition-dependent model of optimal clutch size. *American Naturalist* **162**:110–121.
- Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**:296–298.
- Boulet, M., and D. R. Norris. 2006. The past and present of migratory connectivity. *Ornithological Monographs* **61**:1–13.
- Boulet, M., H. L. Gibbs, and K. A. Hobson. 2006. Integrated analysis of genetic, stable isotope, and banding data reveal migratory connectivity and flyways in the northern Yellow Warbler (*Dendroica petechia*; *Aestiva* group). *Ornithological Monographs* **61**:29–78.
- Bortolotti, G. R., and J. C. Barlow. 1988. Stability of mineral profiles of spruce grouse feathers. *Canadian Journal of Zoology* **66**:1948–1951.
- Bortolotti, G. R., K. J. Szuba, B. J. Naylor, and J. F. Bendell. 1988. Stability of mineral profiles of spruce grouse feathers. *Journal of Wildlife Management* **52**:736–743.
- Braune, B., and M. Simon. 2003. Dioxins, Furans, and non-ortho PCBs in Canadian Arctic seabirds. *Environmental Science and Technology* **37**:3071–3077.
- Brewer, A. D., A. W. Diamond, E. J. Woodsworth, B. T. Collins, and E. H. Dunn. 2000. *The Atlas of Canadian Bird Banding, 1921–95. Volume 1: Doves, Cuckoos and Hummingbirds Through Passerines*. Canadian Wildlife Service Special Publication, Ottawa, Ontario, Canada URL:http://www.cws-scf.ec.gc.ca/publications/spec/atlas_e.cfm.
- Britten, M. W., P. L. Kennedy, and S. Ambrose. 1999. Performance and accuracy evaluation of small satellite transmitters. *Journal of Wildlife Management* **63**:1349–1358.
- Bruderer, B. 1997. The study of bird migration by radar. *Naturewissenschaften* **84**:45–54.
- Cammell, M. E., G. M. Tatchell, and I. P. Woiwod. 1989. Spatial pattern of abundance of the Black bean aphid, *Aphis fabae*, in Britain. *Journal of Applied Ecology* **26**:463–472.
- Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. Feng, T. W. Sherry, and G. R. Graves. 1997. The use of stable isotope tracers for identifying populations of migratory birds. *Oecologia* **109**:32–141.
- Cochran, W. W., H. Mouritsen, and M. Wikelski. 2004. Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* **304**:405–408.
- Crick, H. Q. P. 2004. The impact of climate change on birds. *Ibis* **146**:48–56.

- Cristol, D. A., M. B. Baker, and C. Carbone. 1999. Differential migration revisited: Latitudinal segregation by age and sex class. *Current Ornithology* **15**:33–88.
- de Witt, C. 2002. An overview of brominated flame retardants in the environment. *Chemosphere* **46**:583–624.
- Dingle, H. 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, New York.
- Dingle, H., and V. A. Drake. 2007. What is migration?. *Bioscience* **57**:113–121.
- Donavan, T., J. Buzas, P. Jones, and H. L. Gibbs. 2006. Tracking dispersal in birds: Assessing the potential of elemental markers. *Auk* **123**:500–511.
- Dunn, P. O. 2004. Breeding dates and reproductive performance. *Advances in Ecological Research* **35**:69–87.
- Dunn, P. O., and D. W. Winkler. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London, Series B, Biological Sciences* **266**:2487–2490.
- Fallon, S. M., R. C. Fleisher, and G. R. Graves. 2006. Malarial parasites as geographical markers in migratory birds?. *Biology Letters* **2**:213–216.
- Fry, B. 2006. *Stable Isotope Ecology*. Springer, New York.
- Gauthreaux, S. A., and C. G. Belser. 2003. Radar ornithology and biological conservation. *Auk* **120**:266–277.
- Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland. 2001. The buffer effect and large-scale population regulation in migratory birds. *Science* **412**:436–438.
- Greenberg, R., and P. P. Marra (Eds.). 2005. *Birds of Two Worlds: The Ecology and Evolution of Temperate-Tropical Migration Systems*. Johns Hopkins University Press, Baltimore, MD.
- Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13**:1–21.
- Hario, M., and J. Uuksulainen. 1993. Mercury load according to moulting area in primaries of the nominate race of the Lesser Black-backed Gull. *Larus f. fuscus*. *Ornis Fennica* **70**:32–39.
- Hatch, J. J. 2002. Arctic Tern (*Sterna paradisaea*). In A. Poole and F. Gill (Eds.) *The Birds of North America*, No. 707. The Birds of North America, Inc., Philadelphia, PA.
- Hays, G. C., S. Akesson, B. J. Godley, P. Luschi, and P. Santidrian. 2001. The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour* **61**:1035–1040.
- Heitmeyer, M. E., and L. H. Fredrickson. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence mallard recruitment? *Transactions of the North American Wildlife and Natural Resources Conference* **46**:44–57.
- Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia* **120**:314–326.
- Hobson, K. A. 2003. Making migratory connections with stable isotopes. Pages 379–391. in P. Berthold, E. Gwinner, and E. Sonnenschein (Eds.) *Avian Migration*. Springer-Verlag, Berlin Heidelberg, New York.
- Hobson, K. A. 2005. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *Auk* **122**:1037–1048.
- Hobson, K. A., and L. I. Wassenaar. 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* **109**:142–148.
- Holland, R. A., K. Thorup, M. J. Vonhof, W. W. Cochran, and M. Wikelski. 2006. Bat orientation using Earth's magnetic field. *Nature* **445**:702.
- Janssens, E., T. Dauwe, L. Bervoets, and M. Eens. 2002. Inter- and intraclutch variability in heavy metals in feathers of Great Tit nestlings (*Parus major*) along a pollution gradient. *Archives of Environmental Contaminants and Toxicology* **43**:323–329.
- Jouventin, P., and H. Weimerskirch. 1990. Satellite tracking of Wandering Albatrosses. *Nature* **343**:746–748.

- Kaminski, R. M., and E. A. Gleusing. 1987. Density and habitat related recruitment in mallards. *Journal of Wildlife Management* **51**:141–148.
- Karasov, W. H., and C. Martinez del Rio. 2007. Isotope ecology. Pages 433–478 in *Physiological Ecology*. Princeton University Press, Princeton, New Jersey.
- Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia* **130**:216–221.
- Kelly, J. F., K. C. Ruegg, and T. B. Smith. 2005. Combining isotopic and genetic markers to identify breeding origins of migrant birds. *Ecological Applications* **15**:1487–1494.
- Kelsall, J. P. 1984. The use of chemical profiles from feathers to determine the origins of birds. Pages 501–515 in J. Ledger (Ed.) *Proceedings of the fifth Pan-African Ornithological Congress, Lilongwe, Malawi, 1980*. South African Ornithological Society, Johannesburg.
- Lajtha, K., and R. H. Michener (Eds.). 1994. *Stable Isotopes in Ecology and Environmental Science*. Blackwell Scientific Publications, Oxford.
- Levey, D., and F. G. Stiles. 1992. Evolutionary precursors of long-distance migration: Resource availability and movement patterns in neotropical landbirds. *American Naturalist* **140**:447–476.
- Liu, J., H. Xiao, F. Lei, Q. Zhu, K. Qin, X.-W. Zhang, X.-L. Zhang, D. Zhao, G. Wang, Y. Feng, J. Ma, W. Liu, *et al.* 2005. Highly pathogenic H5N1 influenza virus infection in migratory birds. *Science* **309**:1206–000.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**:1884–1886.
- Marra, P. P., D. R. Norris, S. M. Haig, M. S. Webster, and J. A. Royle. 2006. Migratory connectivity. Pages 157–183. in K. R. Crooks and M. A. Sanjayan (Eds.) *Connectivity Conservation*. Cambridge University Press, New York.
- Martin, T. M., I. Chades, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris. 2007. Optimal conservation of migratory birds. *Public Library of Science, ONE* **2**(8):e571.
- Michener, R. M., and K. Lajtha (eds.). 2007. *Stable Isotopes in Ecology and Environmental Science*, Second Edition. Blackwell Publishing, Oxford.
- Møller, A. P., and W. Fiedler. 2004. Birds and climate change., P. Berthold (Ed.) *In Advances in Ecological Research*, Vol. 35. Elsevier, Oxford, UK.
- Moore, F. R., R. J. Smith, and R. Sandberg. 2005. Stopover ecology and intercontinental migrants: En route problems and consequences for reproductive performance. Pages 251–261. in R. Greenberg and P. Marra (Eds.) *Birds of Two Worlds—the Ecology and Evolution of Migration*. Johns Hopkins University Press, Baltimore, Maryland.
- Murray, M. R., and D. L. Fuller. 2000. A critical review of the effects of marking on the biology of vertebrates. Pages 15–64 in *Research Techniques in Animal Ecology: Controversies and Consequences*. Methods and Cases in Conservation Science (L. Boitani and T. K. Fuller, eds.). Columbia University Press, New York.
- Newton, I. 2006. Advances in the study of irruptive migration. *Ardea* **94**:433–460.
- Nolan, E. D., and V. Ketterson. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). *Ecology* **57**:679–693.
- Norris, D. R., and P. P. Marra. 2007. Seasonal interactions, habitat quality and population dynamics in migratory birds. *Condor* **109**:535–547.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London Series B* **271**:59–64.
- Norris, D. R., P. P. Marra, T. K. Kyser, J. A. Royle, G. J. Bowen, and L. M. Ratcliffe. 2006. Migratory connectivity of a widely distributed Neotropical-Nearctic migratory songbird. *Ornithological Monographs* **61**:14–28.

- Norris, D. R., D. B. Lank, J. Pither, D. Chipley, R. C. Ydenberg, and T. K. Kyser. 2007. Trace elements identify wintering populations of a migratory shorebird. *Canadian Journal of Zoology* **85**:579–583.
- Ochoas-Acuna, H., M. S. Sepulveda, and T. S. Gross. 2002. Mercury in feathers from Chilean birds: Influence of location, feeding strategy, and taxonomic affiliation. *Marine Pollution Bulletin* **44**:340–349.
- Owen, M., and J. M. Black. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *Journal of Animal Ecology* **58**:603–617.
- Parrish, J. R., D. T. Rogers Jr., and F. P. Ward. 1983. Identification of natal locales of Peregrine Falcons (*Falco peregrinus*) by trace element analysis of feathers. *Auk* **100**:560–567.
- Perrins, C. M. 1970. Timing of birds breeding seasons. *Ibis* **112**:242–255.
- Pliny, the Elder. 1855. *The Natural History*. John Bostock, H.T. Riley (Trans.) Taylor and Francis, Red Lion Court, Fleet Street.
- Pulido, F. 2007. The genetics and evolution of avian migration. *BioScience* **57**:165–174.
- Quinn, T. P. 2005. *The Behavior and Ecology and Pacific Salmon and Trout*. American Fisheries Society, Bethesda Maryland and the University of Washington Press, Seattle.
- Ramenofsky, M., and J. C. Wingfield. 2007. Regulation of migration. *BioScience* **57**:135–143.
- Ramos, M. A. 1983. *Seasonal Movements of Bird Populations at a Neotropical Study Site in Southern Veracruz, Mexico*. Ph.D. dissertation. University of Minnesota, Minneapolis.
- Ramos, M. A., and D. W. Warner. 1980. Analysis of North American subspecies of migrant birds wintering in Los Tuxtlas, southern Veracruz, Mexico. Pages 172–180 in A. Keast and E. S. Morton (Eds.) *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation*. Smithsonian Institution Press, Washington, DC.
- Rappole, J. H., S. R. Derrickson, and Z. Hubalek. 2000. Migratory birds and the spread of West Nile virus in the western hemisphere. *Emerging Infectious Diseases* **6**:319–328.
- Reed, K. D., J. K. Meece, J. S. Henkel, and S. K. Shukla. 2003. Birds, migration and emerging zoonoses: West Nile Virus, Lyme Disease, Influenza A and enteropathogens. *Clinical and Medical Research* **1**:5–12.
- Ricklefs, R. E., S. M. Fallon, S. C. Latta, B. L. Swanson, and E. Bermingham. 2005. Migrants and their parasites: A bridge between two worlds. Pages 210–221 in R. Grrenberg and P. MarraM (Eds.) *Birds of Two Worlds*. Johns Hopkins University Press, Baltimore.
- Riley, J. R., A. D. Smith, D. R. Reynolds, A. S. Edwards, J. L. Osborne, I. H. Williams, N. L. Carreck, and G. M. Poppy. 1996. Tracking bees with harmonic radar. *Nature* **379**:27–30.
- Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and nesting success of migratory birds. *Science* **267**:1987–1990.
- Roff, D. A., and D. J. Fairbairn. 2007. The evolution and genetics of migration in insects. *BioScience* **57**:155–164.
- Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: Animal movement and stable isotopes. *Trends in Ecology and Evolution* **19**:256–263.
- Rundel, P. W., J. R. Ehleringer, and K. A. Nagy. 1988. *Stable Isotopes in Ecological Research*. Springer-Verlag, Berlin.
- Salomonsen, F. 1955. The evolutionary significance of bird migration. *Biologiske Meddelesler* **22**:1–62.
- Sanz, J. J., J. Potti, J. Moreno, S. Merino, and O. Frias. 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology* **9**:461–472.
- Shaffer, S. A., Y. Tremblay, J. A. Awkerman, R. W. Henry, S. L. H. Teo, D. J. Anderson, D. A. Croll, B. A. Block, and D. P. Costa. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* **147**:833–843.

- Shaffer, S. A., Y. Tremblay, H. Weimerskirch, D. Scott, D. R. Thompson, P. M. Sager, H. Moller, G. A. Taylor, D. G. Foley, B. A. Block, and D. P. Costa. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences of the United States of America* **103**:12799–12802.
- Sibley, D. A. 2001. *National Audubon Society Sibley Guide to Birds*. Alfred A. Knopf, New York.
- Smith, T. B., S. M. Clegg, M. Kimura, K. C. Ruegg, B. Mila, and I. Lovette. 2005. Molecular and genetic approaches to linking breeding and wintering areas in five Neotropical migrant passerines. Pages 222–234 in R. Grrenberg and P. Marra (Eds.) *Birds of Two Worlds*. Johns Hopkins University Press, Baltimore.
- Stokely, J. M. 2005. *The Feasibility of Utilizing the Cellular Infrastructure for Urban Wildlife Telemetry*. Ph.D. dissertation. Virginia Polytechnical Institute and Virginia State University.
- Szep, T., A. Moller, J. Vallner, B. Kovacs, and D. Norman. 2003. Use of trace elements in feathers of sand martin *Riparia riparia* for identifying moulting areas. *Journal of Avian Biology* **34**:307–320.
- Vega-Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. *Condor* **100**:69–78.
- Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus Major*). *Proceedings of the Royal Society of London Series B—Biological Sciences* **265**:1867–1870.
- Visser, M. E., C. Both, and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research* **35**:89–110.
- Webster, M. S., and P. P. Marra. 2005. The importance of understanding migratory connectivity. Pages 199–209 in R. Greenberg and P. P. Marra (Eds.) *Birds of Two Worlds: The Ecology and Evolution of Temperate-Tropical Migration Systems*. Johns Hopkins University Press, Baltimore, Maryland.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: Unraveling migratory connectivity. *Trends in Ecology and Evolution* **17**:76–83.
- Winkler, D. W., P. O. Dunn, and C. E. McCulloch. 2002. Predicting the effects of climate change on avian life-history traits. *Proceedings of the National Academy of Sciences* **99**:13595–13599.
- Wikelski, M., E. M. Tarlow, A. Raim, R. H. Diehl, R. P. Larkin, and G. H. Visser. 2003. Costs of migration in free-flying songbirds. *Nature* **423**:704.
- Wikelski, M., D. Moskowitz, J. S. Adelman, J. Cochran, D. S. Wilcove, and M. L. May. 2006. Simple rules guide dragonfly migration. *Biology Letters* **2**:325–329.
- Wikelski, M., R. W. Kays, N. Jeremy Kasdin, K. Thorup, J. A. Swenson, and G. W. Smith Jr. 2007. Going wild: What a global small-animal tracking system could do for experimental biologists. *Journal of Experimental Biology* **210**:181–186.