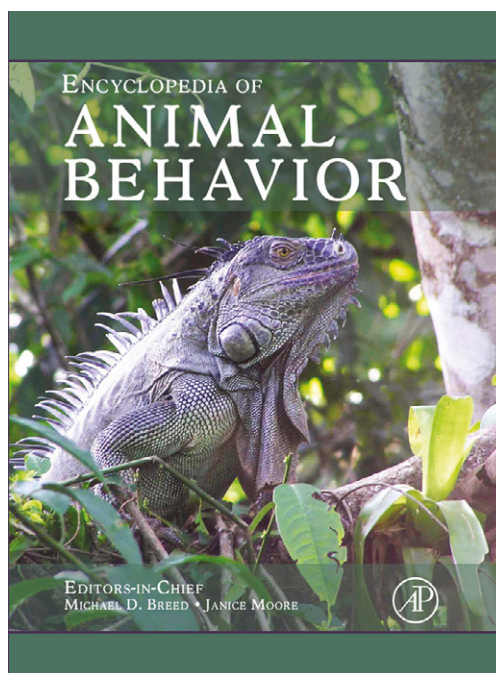


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## Migratory Connectivity

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### Introduction

Migration is a diverse behavior found in all animal taxa, and in its simplest form, is defined as a repeated seasonal movement to and from a breeding area. Animals exhibit several forms of migration, including seasonal migrations across latitudes, altitudinal migrations up and down mountains, migrations that overlap with key life-history stages such as molt, and migrations that can span multiple generations over space and time. This variation can occur within species or between species, but all forms of migration involve movement away from breeding areas and then a return. The geographic linking of individuals or populations between different stages of the annual cycle, including between breeding, migration, and winter stages, is known as *migratory connectivity*. In this article, we will discuss why understanding migratory connectivity is so critical from ecological, evolutionary, and conservation perspectives and also provide descriptions of the various approaches being used to track animals throughout the annual cycle. Most of our examples will be drawn from the bird literature because this is where the understanding is most advanced.

Nearctic–Neotropical migratory birds move north and south between breeding areas in North America and nonbreeding areas in the Caribbean, Middle America, and South America. More specifically, they spend approximately 3–4 months of the year on breeding areas at temperate latitudes. Most species then molt, build fat stores, and migrate south in August and September to a distant and ecologically different location, often in the tropics. It is here that they spend the majority of the annual cycle – 6–8 months. At the end of the stationary portion of the nonbreeding period, they once again build fat stores and leave on spring migration to return to breeding areas. Quantifying migratory connectivity is essential for understanding how events in one period of the annual cycle influence subsequent stages. Such interseasonal effects or ‘seasonal interactions’ are poorly understood within all bird migration systems, in large part because it has been difficult to determine how specific summer and winter populations, along with their stopover locations, are connected throughout the year.

A better understanding of migratory connectivity will allow researchers to follow populations or individuals throughout the annual cycle and thereby address questions regarding the ecological and evolutionary implications of seasonal interactions. The challenge in studying migratory

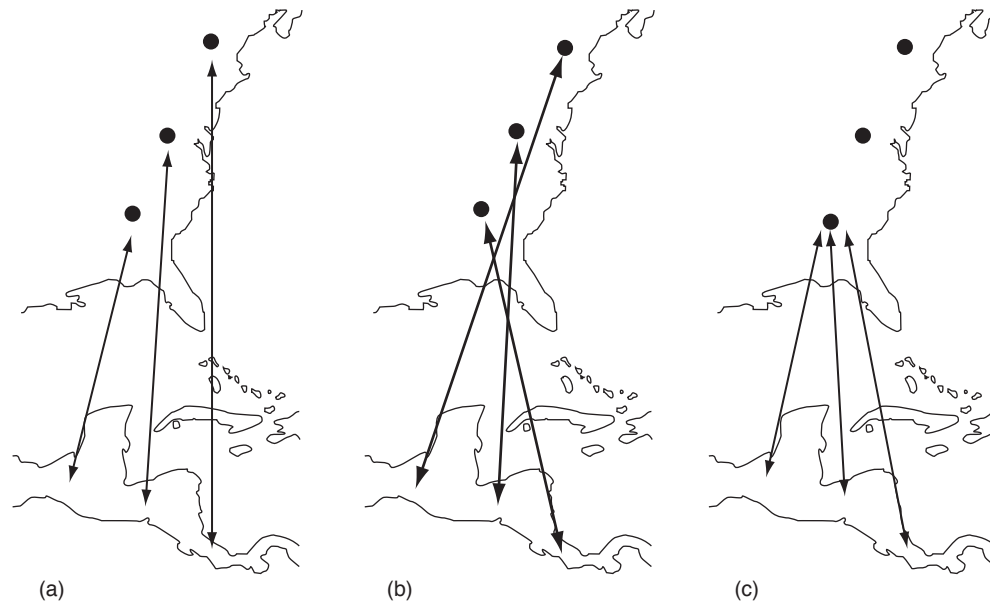
connectivity is to understand not only the geographic connections among periods of the annual cycle but also how these connections influence the ecology, evolution, and conservation of migratory species. Here, we review the ecological and evolutionary considerations of understanding migratory connectivity as well as discuss the advances in marked animal approaches, genetic analyses, and stable isotope chemistry that now make it possible to gain some insights into the population origin of individual birds.

### Why Study Connectivity?

#### Ecological Considerations

The fact that individuals spend time each year in two or more widely separated geographic areas has obvious but poorly studied consequences for population dynamics. The conditions and selective pressures at winter locations are likely to affect individual performance during the breeding season and vice versa. This simple fact has important implications for the ecology, evolution, and conservation of migratory birds. For example, factors and events on the wintering grounds (e.g., weather patterns and deforestation) may affect bird survival and, hence, subsequent recruitment on the breeding grounds. Similarly, differences in reproductive success in summer can lead to changes in the structure of the winter population. Consider an example from a long-distance migratory bird that breeds in Eastern North America. Seasonal interactions and carry-over effects are likely to be most pronounced if summer and winter populations are tightly linked (i.e., if individuals overwintering together in one location also breed near each other in a particular part of the breeding range (**Figure 1(a) and 1(b)**)), but may be much less pronounced if population connections are weak (i.e., if individuals overwintering in one area spread out over a large geographic range for breeding (**Figure 1(c)**)).

Interestingly, if birds originating from three different breeding sites completely segregate on wintering areas, resulting in high migratory connectivity (**Figure 1(a) and 1(b)**), then one could theoretically differentiate between two alternate migration strategies. First, birds could use (1) *leapfrog migration* – where northern wintering populations breed in the southern portions of the breeding range, and southern wintering populations breed in the northern portions of the breeding range (**Figure 1(a)**). This would



**Figure 1** Illustrations of strong (a and b) and weak (c) migratory connectivity for a hypothetical population of Neotropical–Nearctic migratory bird. Strong connectivity may occur as either (a) leapfrog or (b) chain migration strategies as birds travel between tropical wintering and temperate breeding grounds.

result in differential migration distance between populations, where northern wintering populations migrate a comparatively short distance and southern winter populations migrate to northern latitudinal extremes. Alternatively, individuals may use (2) *chain migration* – where northern wintering populations breed in the northern portion of the breeding range and southern wintering populations breed in the southern portion of the breeding range (Figure 1(b)). Migration distance, therefore, is similar between populations. In either case, the result may have profound implications for life-history strategies as well as other aspects of the ecology and evolution of migratory species.

Similarly, large-scale climatic events can have effects on migratory populations throughout the year. For example, recent analyses show that global climate patterns can affect demographic rates (El Niño Southern Oscillation) and, ultimately, population dynamics (climate change). For migratory species, the magnitude of such effects on population dynamics will likely vary with the degree of connectivity between winter and summer populations. There is a need to determine this connectivity, along with detailed modeling efforts, in order to ascertain how focal breeding populations are affected by large and small-scale events affecting various wintering populations (and vice versa). Such information is essential for determining when in the annual cycle populations are most limited and what factors drive population dynamics.

Finally, the scope of natal dispersal will determine the extent to which events in one part of the breeding ground might affect the recruitment and gene flow to other parts.

Source/sink population models are a start for understanding these relationships, but more detailed spatial models that explicitly incorporate migration are required. Interestingly, natal dispersal on breeding areas may be determined in part by events on wintering areas. Using stable-hydrogen isotope ratios in the feathers of American redstarts (*Setophaga ruticilla*) captured as immature birds and again as adults, Colin Studds, Peter Marra, and Kurt Kyser, showed that habitat use during the first tropical nonbreeding season interacts with latitudinal gradients in spring phenology on the temperate breeding grounds to influence the distance traveled on migration and the direction of dispersal by first-year redstarts. Because natural selection acts on these animals throughout the annual cycle, as we gain a better understanding of migratory connectivity, more emphasis should be placed on studying the biology of these animals in the context of where they have come from and where they are going in the next phase of their life cycle.

### Evolutionary Considerations

Individuals of migratory species experience two widely separated and ecologically different habitats during their lifetimes. Selective pressures are likely to vary between these summer and winter habitats, and this may affect the degree to which individuals are ‘locally adapted’ to either habitat. Models of nonmigratory species have shown that the effects of gene flow on local adaptation and niche breadth can be complicated by population dynamics and mating patterns, but few models have explicitly incorporated the effects of migration. Furthermore, for many species

of migratory birds, males and females occupy different habitats on the wintering grounds (sexual habitat segregation) but not on the breeding grounds. Thus, males and females are subject to similar selection pressures in the summer, but different ones in the winter.

The degree of local adaptation is likely to be strongly affected by the strength of connectivity between summer and winter populations. For example, if summer and winter populations are tightly linked, it may be possible for particular populations to become 'well adapted' to both their summer and winter grounds. If, on the other hand, birds from a particular breeding population spread out over the entire winter range (and vice versa), we expect a somewhat poorer fit between the birds and their environment. Likewise, local adaptation on the breeding grounds may be hindered by strong connections among breeding populations via natal dispersal. This expectation is supported by the gene flow studies of nonmigratory species. To our knowledge, the effects of the microevolutionary consequences of migratory connectivity have not been explored in any migratory species, despite the fact that such effects should be more pronounced than in sedentary species.

## How Can We Determine Migratory Connectivity?

### Marked Animal Approaches

Capture–recapture methods developed within the last decade permit direct estimation of movement probabilities of individually marked animals across different locations. The methods involve the use of multistate models in which individual animals are categorized by the location at which they are recaptured or re-sighted. These models permit estimates of different detection probabilities for different locations and estimates of location-specific rates of survival and movement. Although suitable for many types of investigations, data on the return rates of marked individuals to both breeding and wintering grounds have not proven useful for understanding the connectivity of migratory bird populations. The problem is that it is all but impossible to re-sight or recapture the same individuals at multiple locations throughout the annual cycle. Satellite transmitters, unlike traditional markers such as leg bands, offer promise for understanding migratory connectivity. Unfortunately, they are quite expensive (\$3500) and are limited to animals of large body size (>165 g), which excludes all passerine songbirds as well as smaller shorebirds and raptors. For larger birds, satellite transmitters allow the detailed collection of direct information on the movement patterns of individuals over large spatial areas.

Engineers at the British Antarctic Survey have recently developed a miniature and affordable daylight-level data recorder (geolocator) for tracking animals over long

periods of time. These devices weigh as little as 0.8 g, and are rapidly becoming smaller and can be attached to birds by methods similar to long-standing VHF radio-transmitters used in radio-tracking songbirds. Geolocators take consistent readings of daylight timing for 1–2 years. Unlike radio-transmitters, the geolocators must be recovered from returning birds and archived data downloaded. The recovered data are then interpreted to determine the latitude and longitude of the individual bird twice per day for every day the logger was attached and exposed to suitable sunlight. These geolocators have returned accurate and detailed location information on large pelagic birds, and their utility on small migrating songbirds has recently been demonstrated with a single study of the Wood Thrush (*Hylocichla mustelina*) and Purple Martin (*Progne subis*) conducted by ornithologist Bridget Stutchbury. The use of geolocator tags for studies of migratory connectivity and seasonal interactions in small passerine songbirds may thus present an unparalleled opportunity to discover how distant breeding and nonbreeding areas connect and interact in space and time.

### Molecular Genetic Approaches

Because *extrinsic markers*, such as the aforementioned tagging methods, require that the marked individuals be relocated at some point, some researchers have turned their attention to the use of *intrinsic markers* of population origin – that is, markers or indicators that come from the animal itself. One popular approach has been to use molecular genetic markers, because although only some birds have leg bands (or other extrinsic tags), they *all* have DNA. Genetic markers clearly hold considerable potential for the studies of migratory connectivity, but their use is complicated by a number of factors.

The basic logic of most genetic approaches is that, if certain genetic markers (e.g., alleles or haplotypes) are found, say, in one breeding population (X) but not another (Y), then finding those markers in a particular wintering population will indicate some level of connectivity between that wintering population and breeding population X. In some cases, it should also be possible to determine the degree or strength of that connectivity. For example, strong connectivity would be suggested if many individuals in the wintering population had the genetic marker from breeding population X.

This approach hinges on some level of genetic differentiation among breeding populations. Typically, markers will not be unique to particular populations, but instead might vary in frequency across populations. In this case, it is possible to calculate the probability that a wintering individual originated from one breeding population or another (or vice versa) – that individual has a high probability of originating from any population where its genetic markers are common, and a low probability of having

come from populations where those markers are rare. Indeed, a number of sophisticated analytical methods ('assignment tests') have been devised to determine the probability (or likelihood) that an individual came from one population or another, including situations where the actual population of origin may not have been sampled. The strength of these probability calculations, and hence the ability to assign individuals and determine connectivity, depend on both the degree of genetic differentiation among populations (e.g., in the breeding range) and on the number of markers used. In the extreme case of complete differentiation, a particular genetic marker will be found in one population and not others, and hence a single genetic locus can indicate the population of origin. Typically, genetic differentiation among populations will not be so extreme, and a relatively large number of markers may be needed.

In recent years, a number of highly variable (polymorphic) genetic markers have been developed, thereby substantially increasing the likelihood of finding the genetic variation needed to assign individuals to populations and determine connectivity. Microsatellites are a particularly popular class of markers, owing to their typically high levels of polymorphism and ease of use. Moreover, the primary difficulty with using microsatellites – that they need to be developed for each species of interest – is becoming less of a limitation as new high-throughput genomic methodologies (e.g., 454 sequencing) become more widespread. Some studies have also used sequence data for specific loci that are variable enough to show polymorphism within or across populations, such as the highly variable mitochondrial 'control region.' Another potentially useful class of genetic markers that has been used only rarely for the studies of migratory animals is amplified fragment length polymorphism (AFLP). This method simultaneously surveys a large number of genetic loci and typically uncovers substantial variation, which can be used to differentiate among populations. Finally, recent technological advances in genomics have made it possible to scan the genome for single nucleotide polymorphisms (SNPs) which are common and distributed throughout the genome and therefore hold considerable potential for evolutionary and population genetic studies. To date, few studies have used SNPs to study migratory connectivity, though the potential power of these markers makes it likely they will be used in the very near future as costs decrease.

With the development of highly variable markers and sophisticated methods to analyze them, the principal difficulty with molecular genetic approaches to study connectivity is no longer technological, but rather biological. That is, for many organisms, genetic differentiation among populations is very low and may be insufficient for a robust assignment of individuals using genetic markers alone. This is not so much an issue of the markers, but rather the

dispersal behavior of the organisms themselves, as high levels of gene flow will prevent or degrade genetic differentiation among populations. Finding low differentiation among populations is itself informative, as high levels of dispersal between populations suggest low levels of migratory connectivity. However, because it is really natal dispersal that affects genetic differentiation (i.e., how far, on average, an individual moves from where it was born to where it settles and breeds as an adult), high levels of natal dispersal can eliminate genetic differentiation among populations even if adults show very high levels of migratory connectivity, thereby making it difficult to assess the migratory connectivity of adults. Time is another factor affecting genetic differentiation among populations, as it takes some time for genetic differentiation to build up. Thus, migratory organisms that have recently expanded from a smaller population (e.g., since the last Pleistocene glacial maximum) may show limited genetic differentiation among populations.

Because of these factors, several recent studies of Nearctic–Neotropical migratory birds – which are thought to have high levels of natal dispersal and also have undergone recent population expansions – have found limited utility for genetic markers in disentangling migratory connectivity. However, these studies were able to use genetic markers to determine connectivity at broad geographic scales, and higher resolution (i.e., more variable) markers may allow the determination of connectivity at finer scales. In the end, genetic markers may be most useful to studies of migratory species with somewhat limited natal dispersal, and/or in combination with other types of markers.

### **Stable Isotope Approaches**

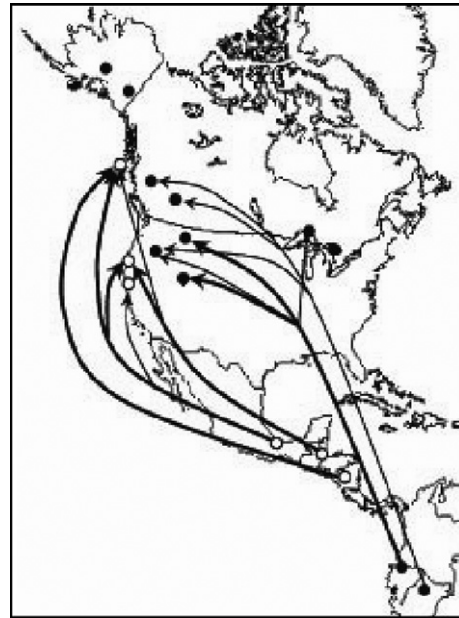
Another technique that relies on intrinsic markers in biological tissues to trace the origin and movement of migratory animals is stable isotope analysis. Stable isotopes are nonradioactive forms of elements that have similar chemical properties but vary in their atomic mass because of differences in the number of neutrons. During geochemical and metabolic processes, the differences in mass cause separation among isotopes of the same element, a phenomenon known as *isotopic fractionation*. Approximately, two-thirds of the elements have more than one stable isotope, but isotopes of carbon ( $^{13}\text{C}$ ), nitrogen ( $^{15}\text{N}$ ), hydrogen ( $^2\text{H}$  or D), and sulfur ( $^{34}\text{S}$ ), are among the most useful for studying migratory connectivity for two reasons. First, their patterns of isotopic fractionation are well understood and vary predictably across broad spatial scales. Second, their high natural abundance allows them to be present at detectable levels in biological tissues. Stable isotopes are analyzed using *isotope ratio mass spectrometry*, and sample results are expressed in  $\delta$  units relative to a standard of known

isotopic composition. For example, the results of carbon isotope analysis are calculated as:  $\delta^{13}\text{C} = \{[(\delta^{13}\text{C}_{\text{unk}}/\delta^{12}\text{C}_{\text{unk}})/(\delta^{13}\text{C}_{\text{std}}/\delta^{12}\text{C}_{\text{std}})] \times 1000\}$ . Some of the most informative research on migratory connectivity has involved multiple stable isotopes or used stable isotopes and genetic markers together, and we will highlight these studies.

Feathers are the most commonly used tissue in stable isotope investigations of migratory connectivity. Most species of migratory birds undergo a complete molt once each year between July and September or near their breeding areas, and the isotopic signatures of foods eaten during this time become incorporated into feathers. Because isotopic signatures are mostly inert once stored in feather tissue, samples collected later during the year provide information about the geographic origin of birds during molt. Each of the aforementioned isotopes provides different potential clues about a bird's molt location. Stable-hydrogen isotopes in growing season precipitation vary strongly with latitude. Stable-carbon isotopes show a similar pattern due to broad-scale differences in plant water use efficiency and photosynthesis strategy. Finally, stable-sulfur isotopes differ between marine and terrestrial environments, making it possible to measure longitudinal origins of molt in species whose habitats extend to coastal regions.

In one of the earliest sets of studies using multiple stable isotopes, Richard Holmes, Page Chamberlain, Dustin Rubenstein, and colleagues, sampled feathers from Black-throated blue warblers at breeding sites from North Carolina to Michigan. As predicted, they found that  $\delta\text{D}$  and  $\delta^{13}\text{C}$  values varied systematically with the latitude of the sampling location. Feathers collected from wintering populations in the Greater Antilles revealed considerable mixing of individuals from a variety of breeding populations, but also indicated strong regional connectivity between wintering and breeding populations. A greater proportion of individuals wintering in the western islands of the Greater Antilles originated from northern breeding populations, whereas those wintering on islands further east were from more southern breeding populations.

When examined alongside molecular genetic markers, analyses of multiple stable isotopes can potentially yield even more refined estimates of migratory connectivity. Jeff Kelly and colleagues analyzed  $\delta\text{D}$ ,  $\delta^{34}\text{S}$ , and mitochondrial DNA (mtDNA) in the feathers of Swainson's thrush at 12 breeding sites throughout North America and 5 winter sites in Mexico, Central, and South America. Analyses of mtDNA indicated the existence of two haplotypes: inland and coastal. Patterns of  $\delta\text{D}$  were particularly useful at distinguishing birds from coastal sites, while variations in  $\delta^{34}\text{S}$  were helpful in separating inland sites. Together, these data revealed that birds with coastal haplotypes migrated to more northern winter sites compared to inland ones, and that birds from northern winter sites



**Figure 2** Map of predicted breeding sites of Swainson's thrushes sampled at five wintering sites. The weight of the arrows reflects the number of individual birds predicted to share that breeding origin. Heavy arrows indicate that 4–6 individuals share the origin; light arrows indicate that 1–3 individuals share that origin.

appeared to migrate shorter distances to southern breeding sites. This latter finding suggested that Swainson's thrushes engage in leapfrog rather than chain migration (Figure 2).

It is important to note that stable isotopes and molecular genetic markers have been used with great success in taxa other than birds. For example, Luciano Valenzuela and coworkers used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  together with mtDNA to identify summer feeding areas in right whales and to understand the behavioral mechanism through which calves learn these locations. Furthermore, individual right whales that shared the same mitochondrial haplotype also had similar  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures. This pattern suggested that individuals from each matrilineal lineage followed the same migratory route to summer feeding locations that they learned from their mothers during their first year of life.

An example using multiple stable isotopes with clear implications for conservation involves Monarch butterflies. The entire population of North American Monarch butterflies spends the winter at approximately ten winter sites in Mexico. Despite over 50 years of intensive study, it remained unknown whether the entire population mixed together at these winter sites or whether there was tighter connectivity between breeding and wintering populations. Len Wassenaar and Keith Hobson sampled  $\delta\text{D}$  and  $\delta^{13}\text{C}$  in butterflies at their natal sites throughout North America and at 13 winter locations in Mexico.

Isotopic signatures indicated that individuals from the Midwestern United States were present at each of the winter sites sampled. However, butterflies with isotopic signatures indicative of more northern breeding areas were present at only two sites, making these locations strong candidates for protection.

Although the isotopic composition of several different tissues has proven to be useful for identifying regional and, potentially, even more localized populations of migratory species, there are several important caveats to this technique. Each isotope carries a unique set of assumptions, and it is necessary to understand these assumptions and to tailor experimental design accordingly. For example, despite its frequent use, the successful use of  $\delta\text{D}$  to unravel migratory connectivity depends on assigning individuals to the geographic location of molt by using a  $\delta\text{D}$  base map developed from 30-year running averaged values as a guide. Therefore, it is not only important to understand the natural history of the study species but also necessary to account for environmental, sampling, and analytical error. Bayesian statistical methods are quickly becoming recognized as an important tool in dealing with this bias because of their ability to incorporate prior information about the potential sources of error into models.

### Future Considerations

Other intrinsic techniques have been attempted but with varying results. For example, populations of blood parasites within migratory species, such as malaria and bacteria, have been used in the studies of migratory connectivity, but these approaches have been met with mixed success. Recently, trace elements have also been explored for their utility in examining migratory connectivity. The growing number of studies showing differences in trace element concentrations among spatially discrete bird populations underscores the future potential of this technique. However, unlike the most often used stable isotopes, trace element signals are not known to change in continuous fashion across physical or environmental gradients. Thus, leveraging trace element data to advance our understanding of migratory connectivity will likely first require detailed mapping of these elements across the breeding and/or wintering ranges of migratory species.

For the time being, as far as smaller-bodied birds are concerned, geolocators, isotopes, and perhaps genetics, will be our best approach. With advances in analytical techniques, the research bottleneck has shifted from the lab to the field: although the isotopic and genetic tools are available, it remains difficult for a single researcher (or team) to collect samples from many hundreds or thousands of individual birds from across the range of a particular species. Hence, as banding studies increase throughout North and South America, Africa, and Asia,

there should be an organized and systematic feather-collection (as well as tissues from other taxa) initiative that will foster studies at scales of sampling intensity that are otherwise impossible to achieve.

In North America alone, approximately 1.2 million songbirds are banded each year. Yet, only in a few instances, are feathers being collected, and there is not yet any systematic effort within the ornithological community to collect and archive such samples. Clearly, this represents a lost opportunity for gaining valuable data. Not only can feathers be informative about extant patterns and processes, but the prospect of collections made over time offer the possibility of tracking temporal changes in breeding and/or wintering ranges of species. Such data would be important to evolutionary biologists interested in microevolutionary processes, population biologists investigating the causes for population declines, as well as conservation biologists concerned about the effects of climate change.

*See also:* Magnetic Orientation in Migratory Songbirds.

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