

## **The Past and Present of Migratory Connectivity**

Authors: Boulet, Marylène, Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina 27708, USA, and Norris, D. Ryan, Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada

Source: Ornithological Monographs No. 61

Published By: American Ornithological Society

URL: <https://doi.org/10.2307/40166835>

---

BioOne Complete ([complete.BioOne.org](http://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



## INTRODUCTION

### THE PAST AND PRESENT OF MIGRATORY CONNECTIVITY

MARYLÈNE BOULET<sup>1,3</sup> AND D. RYAN NORRIS<sup>2</sup>

<sup>1</sup>*Department of Biological Anthropology and Anatomy, Duke University, Durham, North Carolina 27708, USA; and*

<sup>2</sup>*Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 2W1, Canada*

“MIGRATORY CONNECTIVITY” REFERS TO the degree to which two or more periods of the annual cycle are geographically linked. The term was first proposed by a group of scientists during a workshop on “Connectivity of Migratory Birds” in October 2000 sponsored by the National Science Foundation (Webster et al. 2002, Rubenstein and Hobson 2004). The renewed interest in tracking birds over long distances arose, in part, from the application of two intrinsic markers: stable isotopes and genetic markers, such as microsatellites and mitochondrial DNA (mtDNA). Because each individual carries information about its origin in its tissues, the advantage of using intrinsic markers is that an individual needs to be captured only once to estimate its geographic origin in a previous season (Wenink and Baker 1996, Chamberlain et al. 1997, Haig et al. 1997, Hobson and Wassenaar 1997). Measuring migratory connectivity was also driven by the long-standing interest in identifying factors that limit populations in different periods of the annual cycle and understanding how events interact between periods to influence populations (Fretwell 1972, Holmes and Sherry 1992, Sherry and Holmes 1995, Marra et al. 1998). Without knowledge of how populations are spatially distributed between these periods, it is virtually impossible to understand how events in different periods of the year influence abundance (Webster and Marra 2005, Marra et al. 2006). Below, we review the definition of migratory connectivity, briefly outline the history of this field of study, and provide an update on recent studies that have used multiple intrinsic markers to describe migration patterns.

#### A DEFINITION

Migratory connectivity describes the degree to which individuals or populations are geographically arranged among two or more periods of the annual cycle (Webster et al. 2002, Marra et al. 2006). In the simplest sense, the periods of the annual cycle include the breeding season, fall migration, the (stationary) wintering season, and spring migration. “Very strong” or “strong” connectivity refers to the state when all or most individuals from a given area migrate to a single area in the following period of the annual cycle, respectively (Marra et al. 2006; Fig. 1). By contrast, “no connectivity” occurs when individuals from a given area migrate equally to multiple areas the following season (Marra et al. 2006; Fig. 1). In reality, the relative degree of migratory connectivity will likely vary between these two extremes. The concept was initially defined for migratory birds but can readily be applied to any migratory taxa, such as invertebrates, fish, turtles, ungulates, or marine mammals. Migratory connectivity is important for understanding population dynamics, interactions of events between seasons, life-history strategies, and evolution of migration patterns. It is also critical for designing effective conservation plans (see Webster et al. 2002, Webster and Marra 2005; for a detailed review, see Marra et al. 2006).

#### THE PHENOTYPIC AND BANDING PERIOD (PRE-1996)

Although migratory connectivity is relatively new, the concept of linking breeding and nonbreeding regions has a much longer history. Below, we review some of these early contributions.

<sup>3</sup>E-mail: marylene.boulet@duke.edu

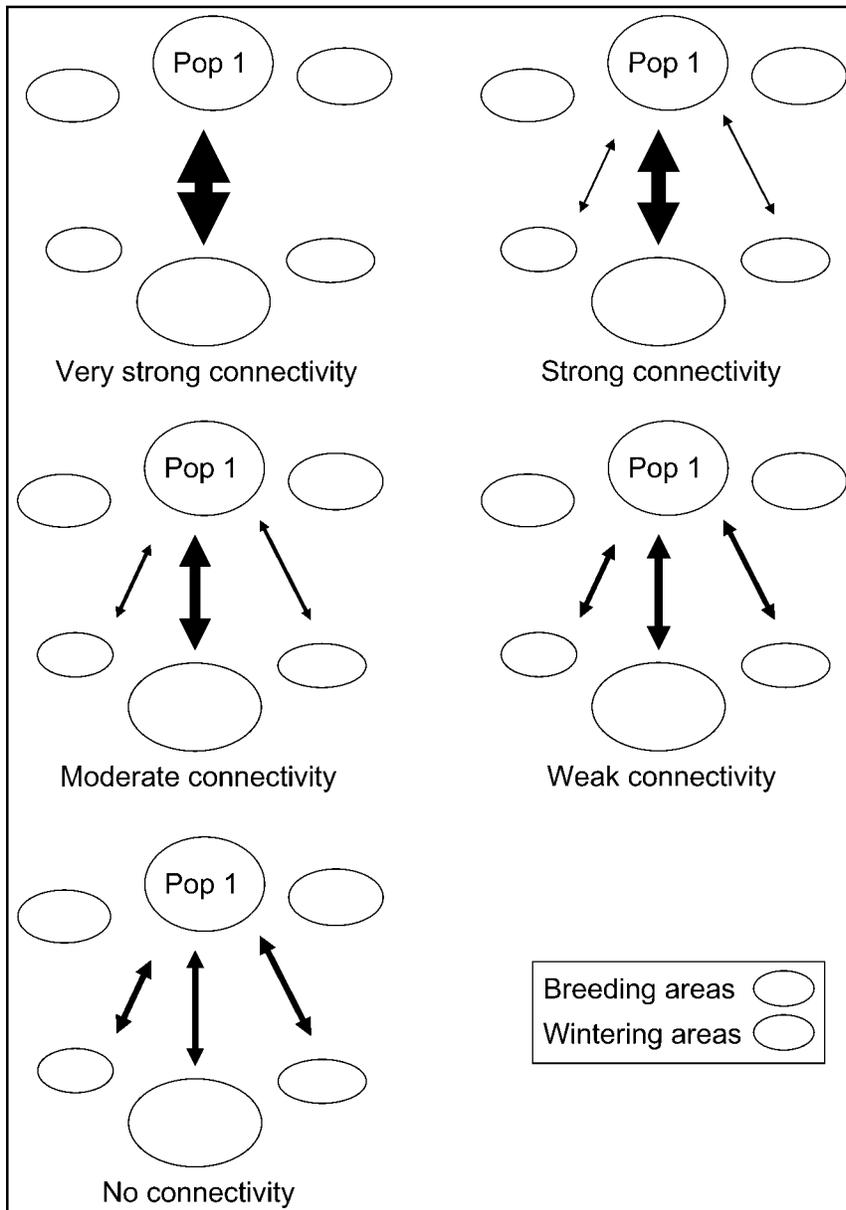


FIG. 1. Theoretical degrees of migratory connectivity in a fictional breeding population. Size of each arrow is proportional to the number of individuals from the breeding Population 1 going to specific wintering areas. The degrees of migratory connectivity range from very strong connectivity (all individuals from a breeding population migrate to a single wintering population), to moderate connectivity (a large proportion of the individuals from a breeding population migrate to a single wintering population), to no connectivity (individuals from a breeding population migrate to different wintering populations in equal proportions). Modified from Webster et al. (2002) and Marra et al. (2006).

*A century of plumage, morphology, and banding data.*—For more than a century, naturalists and taxonomists have used plumage and morphological traits to define geographically distinct subspecies on the breeding grounds (AOU 1998). In some cases, the wintering distributions of subspecies have also been described (Bent 1963), providing some information about the degree of subspecies segregation on the wintering grounds. For example, two groups of the Yellow-rumped Warbler (*Dendroica coronata*) are recognized in North America: the myrtle warbler (*D. coronata*; *coronata* group) breeds from eastern North America to northern British Columbia and Alaska; whereas Audubon's warbler (*D. coronata*; *auduboni* group) breeds from the eastern side of the Rocky Mountains to the Pacific coast. These groups have distinct plumage patterns, and their respective wintering distributions are well known on the basis of taxonomic classifications (Bent 1963, Dunn and Garrett 1997). Because their breeding and wintering distributions show little overlap, migratory connectivity is strong between these groups.

Another example is the Fox Sparrow (*Passerella iliaca*), a polytypic species that can be divided into four major groups based on plumage and morphological variation: the red fox sparrow (*P. iliaca*; *iliaca* group) with a reddish plumage, streaked back, and relatively shorter tail; the sooty fox sparrow (*P. iliaca*; *unalaschensis* group) with a dark-brown plumage, relatively shorter tail, and medium-sized bill; the slate-colored fox sparrow (*P. iliaca*; *schistacea* group) with reddish wings and tail, gray back, long tail, and medium-sized bill; and the thick-billed fox sparrow (*P. iliaca*; *megarhyncha* group) with reddish wings and tail, gray back, long tail, and large bill (Weckstein et al. 2002). The four groups tend to winter in distinct areas, but mixing of two to three groups appears to occur in the westernmost part of their range. Within the sooty fox sparrow group, subspecies segregate latitudinally along the coastal wintering grounds (Swarth 1920, Bell 1997).

Banding programs have existed for about a century in Europe and North America (Brewer et al. 2000, Bairlein 2001, Berthold 2001, Smith 2006). During the first decades of these programs, bird captures and band encounters were mostly of nonpasserine species. By the 1950s, mist nets had become more available, and captures of smaller birds such as songbirds

increased (Bairlein 2001). Reward programs were also implemented to increase band returns of ducks and geese shot by hunters in North America (Berthold 2001). As a result, encounter rates were (and are still) much higher in ducks and geese than in passerine species (Hobson 2003). For example, encounter rate in Northern Pintail (*Anas acuta*) is 11.1%, versus 0.09% in Red-eyed Vireo (*Vireo olivaceus*) (Bird Banding and Encounter Data 1914–2004, Patuxent Wildlife Research Center; see Acknowledgments). The progressive accumulation of band return data led to the publication of banding atlases during the first half of the 20th century and provided sufficient information to define major migratory flyways for some species (Bairlein 2001). For example, Lincoln (1935) defined four migration flyways in North America on the basis of a large-scale analysis of banded waterfowl: the Atlantic, Mississippi, Central, and Pacific flyways. These flyways are still used for managing waterfowl populations and setting hunting regulations (Hawkins et al. 1984).

*Salomonsen's legacy: Toward a comprehensive synthesis of migration patterns.*—Using the combination of band returns, morphology, and plumage patterns among subspecies, Salomonsen (1955) published one of the most comprehensive reviews of migratory connectivity and migration patterns in birds. Although he did not use the term "migratory connectivity," Salomonsen defined "synhiemy" as the state in which different breeding populations mixed freely on the wintering quarters, and "allohiemy" as the state in which breeding populations segregated on wintering quarters. These terms correspond to more recent terms used to describe migratory connectivity (i.e., "no connectivity" and "strong connectivity," respectively; Webster et al. 2002, Marra et al. 2006; Fig. 1). Salomonsen also described four theoretical types of migration systems that would arise from allohiemy or strong connectivity: longitudinal, parallel, leap-frog, and cross-wise migration (Fig. 2A–D). Longitudinal migration describes populations that migrate along the same degree of longitude. Chain migration is a subtype of longitudinal migration, in which populations breeding in the northernmost areas migrate to the northernmost wintering areas (Fig. 2A). Parallel migration occurs when two adjacent populations migrate side-by-side in a parallel way (i.e., along different degrees of longitude; Fig. 2B). Leap-frog migration occurs

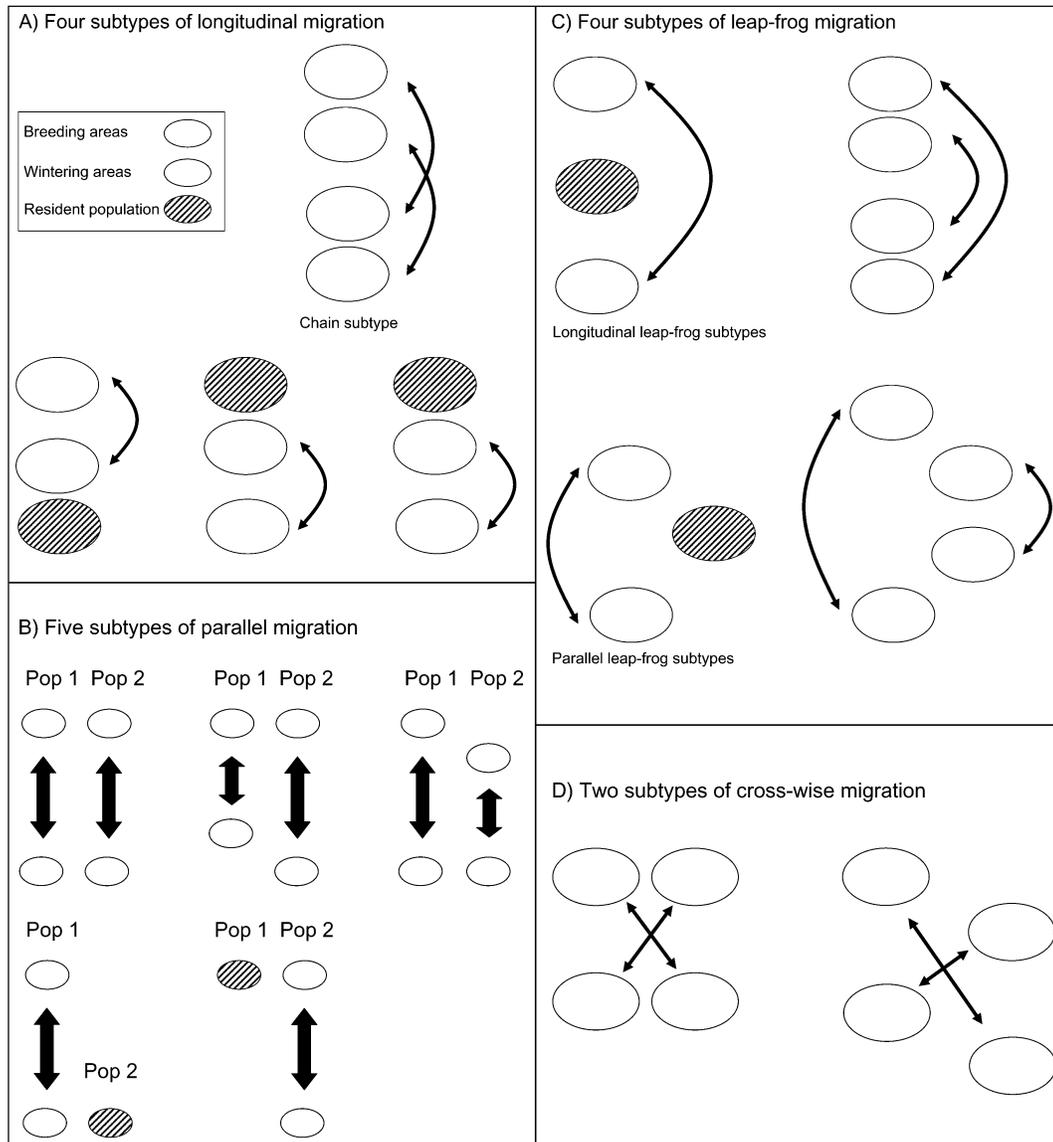


FIG. 2. Salomonsen's theoretical types of migration systems leading to strong connectivity: (A) longitudinal migration, (B) parallel migration, (C) leap-frog migration, and (D) cross-wise migration. Legend is in panel A. Modified from Salomonsen (1955).

when populations occupying the northernmost breeding grounds winter on the southernmost wintering grounds, whereas those breeding farther south winter farther north. In the longitudinal leap-frog subtype, populations migrate along the same longitude, whereas in the parallel leap-frog subtype, populations migrate parallel to each other (Fig. 2C). Finally, cross-wise migration describes cases in which the migration routes of

neighboring populations cross each other—the easternmost breeding population migrates to the westernmost wintering ground, whereas the westernmost breeding population migrates to the easternmost wintering ground (Fig. 2D). Each migration system defined by Salomonsen included subtypes that took into account the presence of nonmigratory populations in the system and the relative geographic locations of

breeding and wintering grounds of populations. For example, one subtype of leap-frog migration describes cases in which a northern breeding population occupies wintering grounds located south of the range of a resident population (Fig. 2C). Another subtype illustrates cases where the range of the resident population is not located along the migration axis of the migratory population (Fig. 2C). These patterns provide schematized models to which scientists can refer for describing complex migration patterns and understanding the evolutionary significance of factors that promote segregation (Boulet et al. 2006).

*Toward the need for developing new markers.*— Between the 1950s and late 1990s, phenotypic markers and banding data were still the most common techniques for assessing the degree of migratory connectivity and studying migration patterns. One of the most detailed studies was undertaken in southern Veracruz (Mexico) in the 1970s by Ramos (1983), who studied migration patterns in nine Nearctic–Neotropical migrant species. He captured, examined, and measured individuals during migration and the stationary wintering period. He then compared these individuals with breeding specimens, which allowed him to describe differential patterns of spatial segregation between species, subspecies, age classes, and sex. He also recorded the date of passage of birds during migration to study differences in timing of migration between subspecies. For example, he showed that southern subspecies of Swainson's Thrush (*Catharus ustulatus*) migrated earlier in spring than northern subspecies in Veracruz. His data revealed that, within a given species, many subspecies that segregated on the breeding grounds mixed during migration or during the stationary wintering period (Ramos and Warner 1980, Ramos 1983). However, because some species lacked clear intraspecific differentiation, the degree of migratory connectivity could not be measured.

The contribution of banding data to our knowledge of migratory connectivity and migration patterns was significant during this period (Brewer et al. 2000, Bairlein 2001). In species for which encounter data were available, spatial analysis and mapping of encounters detected migratory connectivity and spatial or temporal patterns of migration, such as migration routes in White Stork (*Ciconia ciconia*), loop migration in Pied Flycatcher (*Ficedula hypoleuca*), parallel

migration in Chaffinch (*Fringilla coelebs*), and frequency of admigration (switch between flyways) in Green-winged Teal (*Anas crecca*) (Bairlein 2001, Guillemain et al. 2005).

Nevertheless, assessing migratory connectivity and describing migration systems for small-bodied passerines was still challenging, especially in species characterized by limited plumage and morphological differentiation and low band encounters. Among those species are the migratory wood warblers (Parulidae). These species are Nearctic–Neotropical migrants (i.e., they breed in Canada and the United States and migrate southward to overwinter in Mexico, Central America, or South America; Hayes 1995). Within the migratory wood warblers, 65% (32 of 50) of species are monotypic, 30% (15 of 50) of species include 2–4 subspecies, and only 6% (3 of 50) of species include  $\geq 5$  subspecies (Dunn and Garrett 1997). Banding encounters are often  $< 1\%$  in wood warblers; for example, the encounter rate is 0.04% in Black-throated Blue Warbler (*Dendroica caerulescens*) and Wilson's Warbler (*Wilsonia pusilla*) (Bird Banding and Encounter Data 1914–2004, Patuxent Wildlife Research Center; see Acknowledgments). This has led to efforts to find alternative techniques to document connectivity in these species (Webster et al. 2002, Hobson 2005).

#### THE INTRINSIC MARKER PERIOD (1996 TO PRESENT)

In 1996–1997, four influential papers demonstrated that intrinsic markers could be used to estimate the origin of birds in previous periods of the annual cycle. Using mtDNA lineage-specific differences in Dunlin (*Calidris alpina*) populations, Wenink and Baker (1996) revealed that adjacent breeding populations of distinct lineages mixed to some degree on staging and wintering areas. Haig et al. (1997) examined genetic population differentiation in nine shorebird species, including Dunlin, using randomly amplified DNA polymorphism (RADP) markers. Levels of global population differentiation varied between species, but assigning individuals to putative breeding populations was possible in some cases. Chamberlain et al. (1997) and Hobson and Wassenaar (1997) measured stable hydrogen isotope ratios ( $\delta D$ ) in feathers of Nearctic–Neotropical migratory birds. They independently demonstrated that  $\delta D$  values of flight feathers grown on breeding habitats

correlate with  $\delta D$  values of rainfall collected during the growing season. In addition,  $\delta D$  ratios of rainfall varied along a latitudinal gradient across eastern and central North America. Thus,  $\delta D$  ratios of feathers represent a signature of the environment in which the feathers were grown and can be used as a latitudinal marker to track migratory birds. However, in western North America, patterns of  $\delta D$  ratios are much more variable at a regional scale because of rain-shadow effects created by the Rocky Mountains (see map in Hobson and Wassenaar 1997) and, thus, may not be as informative in some western species (Wunder et al. 2005). Chamberlain et al. (1997) showed that stable carbon isotope ratios ( $\delta^{13}C$ ) in bird tissue also varied along a latitudinal gradient and that stable strontium isotope ratios ( $\delta^{84}S$ ) varied according to the geological age of bedrock.

In 2000, the "Connectivity of Migratory Birds" workshop gathered leading scientists for discussions on the issue of how to best estimate the connectivity of migratory animals. One of the major outcomes of the workshop was the publication of a joint paper in which "migratory connectivity" was formally defined (Webster et al. 2002). This workshop was followed by the international conference, "Birds of Two Worlds," which included a symposium on migratory connectivity. The proceedings were recently published in the book *Birds of Two Worlds: The Ecology and Evolution of Migration* (Greenberg and Marra 2005).

Since that period, there has been a growing and sustained interest in using modern techniques to describe patterns of migratory connectivity in a wide variety of species. To date, most studies have focused on raptors, shorebirds, and passerines. For large species like raptors, ducks, geese, and cranes, satellite telemetry technology is also available for tracking movements of individual migrants over large distances with great precision (Fuller et al. 1998, Hake et al. 2001, Higuchi et al. 2004). Additional techniques, such as trace elements (Szép et al. 2003, Donovan et al. 2006), heavier stable isotopes (Hobson 2005), and genetic markers developed from avian parasites or viruses (Ricklefs et al. 2005), have also been proposed.

#### MODEL SPECIES AND CURRENT KNOWLEDGE

Studies assessing migratory connectivity and migration patterns with more than one

type of marker are not yet very common. In Table 1, we summarize the major findings of migratory connectivity studies that used a combination of genetic markers, stable isotopes, banding encounters, or morphology. Our review includes 25 studies and 12 species that breed in Europe and North America. Studies focusing exclusively on stable isotope markers were not included and are reviewed in Hobson (2003). In some instances, a pilot study using a single type of marker was followed up by an additional study using a different marker. For example, Kimura et al. (2002) measured migratory connectivity in the Wilson's Warbler using an mtDNA marker, and they observed strong longitudinal segregation between two lineages throughout the annual range. Clegg et al. (2003) examined migratory connectivity in the same species but used microsatellite markers and  $\delta D$  ratios to refine the continental resolution obtained by mtDNA. Although  $\delta D$  ratios added a complementary latitudinal resolution, microsatellite markers did not provide additional resolution, because they showed less genetic structure between populations than mtDNA. Thus, the addition of a marker does not necessarily translate into increased resolution.

Strong evidence for a parallel migration system has been observed in four species: Dunlin, Swainson's Thrush, northern yellow warbler (*Dendroica petechia; aestiva* group), and Wilson's Warbler (see Table 1). In all cases, the pattern was detected by an mtDNA marker, which often offers a longitudinal (east-west) resolution. However, DNA markers sometimes lack the power to detect structure between groups that recently differentiated, such as in the Black-throated Blue Warbler (Davis et al. 2006). Chain and leap-frog migration patterns have typically been detected by  $\delta D$  ratios, probably because this marker has a latitudinal (north-south) resolution in central and eastern North America, and these patterns describe latitudinal segregation of populations (Clegg et al. 2003, Smith et al. 2003, Norris et al. 2006a). Cross-wise migration has been detected once with a combination of stable isotope markers that had a latitudinal resolution on the breeding grounds and a longitudinal resolution on the wintering grounds (Rubenstein et al. 2002). Varying levels of admixture—from "no connectivity" to "very strong connectivity"—have been observed at stopover sites or at wintering sites. However,

TABLE 1. List of species in which more than one type of marker was used to assess migratory connectivity and migration patterns. Information about annual ranges and ecology of species was obtained from Cramp and Perrins (1993), Dunn and Garrett (1997), and Evans Mack and Yong (2000). “Long-distance migrant” refers to species migrating  $\geq 4,000$  km (broadly speaking) during a migration season (e.g., from Canada to Mexico, Central America or South America). “Short-distance migrant” species migrate  $< 4,000$  km per migration season and usually do not encounter large water-body obstacles (e.g., Canada to southern United States). See Figure 1 for illustrations and definitions of the different degrees of connectivity and Figure 2 for illustrations of migration systems.

Species	Annual range	Migratory and feeding guilds	Markers	Major patterns (corresponding references)
King Eider ( <i>Somateria spectabilis</i> )	Breeds: Arctic Winters: northern seas	Short-distance migrant Piscivore	$\delta D$ , recoveries (from dead individuals)	From $\delta D$ data: admixture of two wintering populations on a single breeding site, but in unequal proportions; suggests weak connectivity (17). From recovery data: admixture of two wintering populations on a single breeding site, but in equal proportions; suggests no connectivity. Discrepancies between markers possibly because of stronger hunting pressures in one wintering area (17).
Sharp-shinned Hawk ( <i>Accipiter striatus</i> )	Breeds: North America Winters: USA, Mexico, Central America, West Indies, Bahamas	Short- to long-distance migrant, some populations are resident Carnivore	$\delta D$ , banding encounters, morphology	Chain migration in hatch-year birds in fall (21).
Dunlin ( <i>Calidris alpina</i> )	Breeds: Arctic Winters: Atlantic and Pacific coasts, Mediterranean coasts, Black Sea, coasts of Middle East	Long-distance migrant Feeds on invertebrates	mtDNA, RADP, morphology	Evidence of links between two spring stopovers and western breeding populations (11). Varying degrees of admixture of adjacent mtDNA lineages along flyways suggest moderate to strong connectivity (depending on regions) (24). Parallel migration system in Eurasia (24, 25).
Red Knot ( <i>Calidris canutus</i> )	Breeds: Arctic Winters: Atlantic and Pacific coasts, Oceania coasts	Long-distance migrant Feeds on invertebrates	$\delta^{13}C$ , $\delta^{15}N$ , mtDNA, banding encounters	No genetic differentiation to moderate significant differentiation ( $F_{ST} = 0.000-0.270$ ) between subspecies in mtDNA (5). <sup>a</sup> Admixture of three wintering populations (but not equally represented) on a spring stopover (Delaware Bay) (1).
Willow Warbler ( <i>Phylloscopus trochilus</i> )	Breeds: Europe Winters: Africa	Long-distance migrant Insectivore	$\delta^{13}C$ , $\delta^{15}N$ , mtDNA, microsat, AFLP, banding encounters, morphology	Stable isotope indicators of African winter quarters of two subspecies suggest strong connectivity and segregation between subspecies on the wintering grounds (7). Isotopic segregation concordant with morphology and an AFLP marker, but not with microsatellite or mtDNA markers (2, 3, 7).

TABLE 1. Continued.

Species	Annual range	Migratory and feeding guilds	Markers	Major patterns (corresponding references)
Swainson's Thrush ( <i>Catharus ustulatus</i> )	Breeds: North America Winters: Mexico, Central America, South America	Long-distance migrant Insectivore	$\delta D$ , $\delta^{13}C$ , $\delta^{34}S$ , mtDNA, banding encounters	Very strong connectivity and segregation between two mtDNA lineages (20). Parallel migration system with one lineage migrating over longer distances than the other (13, 20). Broad catchment regions of boreal forests at two stopover sites (Ontario and Manitoba) (23). Possible connectivity along a latitudinal gradient based on $\delta D$ data and limited wintering sampling (13).
Northern yellow warbler ( <i>Dendroica petechia</i> ; <i>aestiva</i> group) (migratory form)	Breeds: North America Winters: Mexico, Central America and South America	Long-distance migrant Insectivore	$\delta D$ , mtDNA, microsat, banding encounters	Strong connectivity and segregation between two mtDNA lineages (4). No genetic differentiation to weak but significant differentiation ( $F_{ST} = 0.000-0.031$ ) between eight breeding populations at microsatellite markers (10). Parallel migration system (4). Possibility of a leap-frog migration system between highly migratory and less-migratory lineages (4). Birds breeding in northernmost part of the breeding range migrate first in fall (New Mexico) (14).
Black-throated Blue Warbler ( <i>Dendroica caerulescens</i> )	Breeds: Eastern North America Winters: Bahamas, Greater Antilles	Long-distance migrant Insectivore	$\delta D$ , $\delta^{13}C$ , $\delta^{87}Sr$ , mtDNA, microsat	No genetic differentiation to weak but significant differentiation ( $F_{ST} = 0.005-0.029$ ) between four breeding populations at microsat markers (9), no significant genetic differentiation in mtDNA (9). <sup>b</sup> Moderate connectivity and latitudinal segregation on wintering grounds based on $\delta D$ and $\delta^{13}C$ data (19). Cross-wise migration (19). Regional admixture of different breeding locales on wintering sites (6, 19).
American Redstart ( <i>Setophaga ruticilla</i> )	Breeds: North America Winters: Mexico, Central America, northern South America, Bermuda, West Indies	Long-distance migrant Insectivore	$\delta D$ , banding encounters	Moderate to strong connectivity (depending on scale and regions) (18). Possibility of a parallel migration system across the range based on longitudinal variation of $\delta D$ ratios (18). Chain migration within Caribbean region based on latitudinal variation of $\delta D$ ratios suggests regional connectivity (18).

TABLE 1. Continued.

Species	Annual range	Migratory and feeding guilds	Markers	Major patterns (corresponding references)
Common Yellowthroat ( <i>Geothlypis trichas</i> )	Breeds: North America Winters: southern USA to Central America, most of West Indies	Long-distance migrant Insectivore	δD, mtDNA	Possibility of moderate to strong connectivity and segregation between two mtDNA lineages based on limited wintering sampling (22). Birds breeding in southernmost part of the breeding range migrate first in fall (New Mexico) (14).
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	Breeds: North America Winters: Mexico, Central America	Long-distance migrant Insectivore	δD, mtDNA, microsat	Moderate connectivity and some degree of wintering admixture between two mtDNA lineages (15). Parallel migration system (15). Leap-frog migration system within western mtDNA lineage (8). No genetic differentiation to moderate significant differentiation ( $F_{ST} = 0.000-0.156$ ) between eight breeding populations in microsat markers (8). Birds breeding in northernmost part of the breeding range migrate first in fall (New Mexico) (12).
White-throated Sparrow ( <i>Zonotrichia albicollis</i> )	Breeds: North America Winters: south USA.	Short-distance migrant Granivore	δD (tail and head feathers <sup>c</sup> ), banding encounters	Broad array of breeding and wintering catchment areas in a stopover site in Manitoba (16). <sup>c</sup> Extensive mixing of breeding populations from the catchment area on the wintering ground (showed by no relationship between tail and head δD), suggests no connectivity (16). Possible parallel migration system based on east-west segregation of banding encounters (16).

<sup>a</sup> $F_{ST}$  is an index of population differentiation ranging from 0 (no differentiation) to 1 (extreme differentiation).

<sup>b</sup>Lack of significant genetic differentiation precludes the use of this marker for assessing migratory connectivity.

<sup>c</sup>δD of tail feathers are indicators of wintering area, because feathers are grown on wintering grounds.

Abbreviations: δD = stable hydrogen ratio, δ<sup>13</sup>C = stable carbon ratio, δ<sup>15</sup>N = stable nitrogen ratio, δ<sup>87</sup>Sr = stable strontium ratio, mtDNA = mitochondrial DNA marker, microsat = microsatellite marker, AFLP = amplified fragment length polymorphism DNA marker, RAPD = random amplification of polymorphic DNA.

References: (1) Atkinson et al. 2005, (2) Bensch et al. 1999, (3) Bensch et al. 2002, (4) Boulet et al. 2006, (5) Buehler and Baker 2005, (6) Chamberlain et al. 1997, (7) Chamberlain et al. 2000, (8) Clegg et al. 2003, (9) Davis et al. 2006, (10) Gibbs et al. 2000, (11) Haig et al. 1997, (12) Kelly et al. 2002, (13) Kelly et al. 2005, (14) Kelly 2006, (15) Kimura et al. 2002, (16) Mazerolle et al. 2005, (17) Mehl et al. 2004, (18) Norris et al. 2006a, (19) Rubenstein et al. 2002, (20) Ruegg and Smith 2002, (21) Smith et al. 2003, (22) Smith et al. 2005, (23) Wassenaar and Hobson 2001, (24) Wenink and Baker 1996, (25) Wennerberg 2001.

the wood warbler species included in Table 1 (northern yellow warbler, Black-throated Blue Warbler, American Redstart [*Setophaga ruticilla*], Common Yellowthroat [*Geothlypis trichas*], Wilson's Warbler) tended to have similar degrees of migratory connectivity. Thus, while no generalization can be made about migratory connectivity across all species, a large-scale pattern of moderate to strong connectivity emerged from the wood warblers.

One of the major challenges when using multiple markers to describe patterns of connectivity is how to integrate information derived from different types of data. Although banding data were generally processed the same way (i.e., by mapping trajectories), the integration of genetic and stable isotope data has been treated differently. For example, Kelly et al. (2005) used a quadratic discriminant function analysis to assign individuals to discrete sampling sites, whereas Boulet et al. (2006) assigned individuals to their region of origin by overlaying geographic-information-system maps derived from genetic and stable hydrogen data. Likelihood-based assignment methods integrating isotopic information with prior probabilities of assignment related to relative abundance (using Bayes's rule) are also emerging (Royle and Rubenstein 2004, Wunder et al. 2005, Norris et al. 2006a). Other challenges include developing robust tests of assumptions related to the application of intrinsic markers and using information on connectivity to understand the ecology and evolution of migratory species (Norris et al. 2006b). For example, in some migrant species of western North America, juveniles molt their feathers near their natal grounds then directly migrate to the wintering grounds, whereas adults undertake a molt migration to more southern areas and migrate to the wintering grounds once their molt is completed (Voelker and Rohwer 1998, Butler et al. 2002). In these species, juveniles would have, on average, lower  $\delta D$  ratios than adults, and the  $\delta D$  ratios of adults would not be an indicator of the breeding grounds but of the molting grounds.

The following papers examine migratory connectivity and migration patterns in two long-distance migratory songbirds with trans-continental distributions across their breeding and wintering grounds: the American Redstart (Norris et al. 2006a) and the northern yellow warbler (Boulet et al. 2006). These studies

contribute to the knowledge of migratory connectivity by exploring new methodological approaches, combining multiple intrinsic and extrinsic markers, providing extensive spatial coverage, and uncovering unique patterns of migratory connectivity. The last paper of this monograph (Norris et al. 2006b) outlines specific research needs for future migratory connectivity studies.

#### ACKNOWLEDGMENTS

We thank J. Faaborg, Editor of Ornithological Monographs, for proposing this introduction and commenting on the manuscript. We thank M. B. Wunder for stimulating discussions about stable isotope markers. M. B. was supported by a postdoctoral fellowship from the Natural Sciences and Engineering Research Council of Canada. D.R.N. was supported by postdoctoral fellowships from the Natural Sciences and Engineering Research Council of Canada and the Izaak Walton Killiam Memorial Fund.

For Bird Banding and Encounter Data 1914–2004, Patuxent Wildlife Research Center, Laurel, Maryland, see [www.pwrc.usgs.gov/BBL/homepage/spec.htm#6520](http://www.pwrc.usgs.gov/BBL/homepage/spec.htm#6520).

#### LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1998. Checklist of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.
- ATKINSON, P. W., A. J. BAKER, R. M. BEVAN, N. A. CLARK, K. B. COLE, P. M. GONZALEZ, J. NEWTON, L. J. NILES, AND R. A. ROBINSON. 2005. Unravelling the migration and moult strategies of a long-distance migrant using stable isotopes: Red Knot *Calidris canutus* movements in the Americas. *Ibis* 147:738–749.
- 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.
- BENSCH, S., S. ÅKESSON, AND D. E. IRWIN. 2002. The use of AFLP to find an informative SNP: Genetic differences across a migratory divide in Willow Warblers. *Molecular Ecology* 11: 2359–2366.
- BENSCH, S., T. ANDERSSON, AND S. ÅKESSON. 1999. Morphological and molecular variation across a migratory divide in Willow Warblers, *Phylloscopus trochilus*. *Evolution* 53:1925–1935.
- BENT, A. C. 1963. Life Histories of North American Wood Warblers. Dover, New York.
- BERTHOLD, P. 2001. Bird Migration: A General Survey, 2nd ed. Oxford University Press, London.

- 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). Pages 29–78 in *Patterns of Migratory Connectivity in Two Nearctic–Neotropical Songbirds: New Insights from Intrinsic Markers* (M. Boulet and D. R. Norris, Eds.). Ornithological Monographs, no. 61.
- BREWER, D., A. DIAMOND, E. J. WOODSWORTH, B. T. COLLINS, AND E. H. DUNN. 2000. Canadian Atlas of Bird Banding. Canadian Wildlife Service, Environment Canada, Ottawa, Ontario.
- BUEHLER, D. M., AND A. J. BAKER. 2005. Population divergence times and historical demography in Red Knots and Dunlins. *Condor* 107:497–513.
- BUTLER, L. K., M. G. DONAHUE, AND S. ROHWER. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): Age effects, aerodynamics, and conservation implications. *Auk* 119:1010–1023.
- CHAMBERLAIN, C. P., S. BENSCH, X. FENG, S. ÅKESSON, AND T. ANDERSSON. 2000. Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. *Proceedings of the Royal Society of London, Series B* 267:43–48.
- CHAMBERLAIN, C. P., J. D. BLUM, R. T. HOLMES, X. FENG, T. W. SHERRY, AND G. R. GRAVES. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141.
- CLEGG, S. M., J. F. KELLY, M. KIMURA, AND T. B. SMITH. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's Warbler (*Wilsonia pusilla*). *Molecular Ecology* 12:819–830.
- CRAMP, S., AND C. M. PERRINS, Eds. 1993. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic*, vol. VII. Flycatchers to Shrikes. Oxford University Press, Oxford.
- DAVIS, L. A., E. H. ROALSON, K. L. CORNELL, K. D. McCLANAHAN, AND M. S. WEBSTER. 2006. Genetic divergence and migration patterns in a North American passerine bird: Implications for evolution and conservation. *Molecular Ecology* 15:2141–2152.
- DONOVAN, 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, J. L., AND K. L. GARRETT. 1997. *Peterson Field Guide to Warblers of North America*. Houghton Mifflin, New York.
- EVANS MACK, D., AND W. YONG. 2000. Swainson's Thrush (*Catharus ustulatus*). In *The Birds of North America*, no. 540 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- FRETWELL, S. D. 1972. *Populations in a Seasonal Environment*. Princeton University Press, Princeton, New Jersey.
- FULLER, M. R., W. S. SEEGAR, AND L. S. SCHUECK. 1998. Routes and travel rates of migrating Peregrine Falcons *Falco peregrinus* and Swainson's Hawks *Buteo swainsoni* in the western hemisphere. *Journal of Avian Biology* 29:433–440.
- GIBBS, H. L., R. J. G. DAWSON, AND K. A. HOBSON. 2000. Limited differentiation in microsatellite DNA variation among northern populations of the Yellow Warbler: Evidence for male-biased gene flow? *Molecular Ecology* 9:2137–2147.
- GREENBERG, R., AND P. P. MARRA. 2005. *Birds of Two Worlds: The Ecology and Evolution of Migration*. Johns Hopkins University Press, Baltimore, Maryland.
- GUILLEMAIN, M., N. SADOUL, AND G. SIMON. 2005. European flyway permeability and abmigration in Teal *Anas crecca*, an analysis based on ringing recoveries. *Ibis* 147:688–696.
- HAIG, S. M., C. L. GRATTO-TREVOR, T. D. MULLINS, AND M. A. COLWELL. 1997. Population identification of western hemisphere shorebirds throughout the annual cycle. *Molecular Ecology* 6:413–427.
- HAKE, M., N. KJELLÉN, AND T. ALERSTAM. 2001. Satellite tracking of Swedish Ospreys *Pandion haliaetus*: Autumn migration routes and orientation. *Journal of Avian Biology* 32:47–56.
- HAWKINS, A. S., R. C. HANSON, H. K. NELSON, AND H. M. REEVES. 1984. *Flyways: Pioneering Waterfowl Management in North America*. U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C.
- HAYES, F. E. 1995. Definitions for migrant birds: What is a Neotropical migrant? *Auk* 112:521–523.
- HIGUCHI, H., J. P. PIERRE, V. KREVER, V. ANDRONOV, G. FUJITA, K. OZAKI, O. GOROSHKO, M. UETA, S. SMIRENSKY, AND N. MITA. 2004. Using a remote technology in conservation: Satellite tracking White-naped Cranes in Russia and Asia. *Conservation Biology* 18:136–147.
- HOBSON, K. A. 2003. Making migratory connections with stable isotopes. Pages 379–392 in *Avian Migration* (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Berlin.
- 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.
- HOLMES, R. T., AND T. W. SHERRY. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection, and conservation. Pages 563–575 *in* Ecology and Conservation of Neotropical Migrant Landbirds (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- KELLY, J. F. 2006. Stable isotope evidence links breeding geography and migration timing in wood warblers (Parulidae). *Auk* 123:431–437.
- 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.
- KIMURA, M., S. M. CLEGG, I. J. LOVETTE, K. R. HOLDER, D. J. GIRMAN, B. MILÁ, P. WADE, AND T. B. SMITH. 2002. Phylogeographical approaches to assessing demographic connectivity between breeding and overwintering regions in a Nearctic–Neotropical warbler (*Wilsonia pusilla*). *Molecular Ecology* 11:1605–1616.
- LINCOLN, F. C. 1935. The waterfowl flyways of North America. U.S. Department of Agriculture, circular no. 342.
- 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. WEBSTER, AND J. A. ROYLE. 2006. Migratory connectivity. Pages 157–183 *in* Connectivity Conservation (K. Crooks and M. Sanjayan, Eds.). Cambridge University Press, New York.
- MAZEROLLE, D. F., K. A. HOBSON, AND L. I. WASSENAAR. 2005. Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of White-throated Sparrows at a migration monitoring station. *Oecologia* 144:541–549.
- MEHL, K. R., R. T. ALISAUSKAS, K. A. HOBSON, AND D. K. KELLETT. 2004. To winter east or west? Heterogeneity in winter philopatry in a central-Arctic population of King Eiders. *Condor* 106: 241–251.
- NORRIS, D. R., P. P. MARRA, T. K. KYSER, G. J. BOWEN, AND L. M. RATCLIFFE. 2006a. Migratory connectivity of a widely distributed songbird, the American Redstart (*Setophaga ruticilla*). Pages 14–28 *in* Patterns of Migratory Connectivity in Two Nearctic–Neotropical Songbirds: New Insights from Intrinsic Markers (M. Boulet and D. R. Norris, Eds.). Ornithological Monographs, no. 61.
- NORRIS, D. R., M. B. WUNDER, AND M. BOULET. 2006b. Perspectives in migratory connectivity. Pages 79–88 *in* Patterns of Migratory Connectivity in Two Nearctic–Neotropical Songbirds: New Insights from Intrinsic Markers (M. Boulet and D. R. Norris, Eds.). Ornithological Monographs, no. 61.
- RAMOS, M. A. 1983. Seasonal movements of bird populations at a Neotropical site in southern Veracruz, Mexico. Ph.D. dissertation, Department of Zoology, University of Minnesota, Minneapolis.
- RAMOS, M. A., AND D. W. WARNER. 1980. Analysis of North America subspecies of migrant birds wintering in Los Tuxtlas, southern Veracruz, Mexico. Pages 173–180 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.
- 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* Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Eds.). John Hopkins University Press, Baltimore, Maryland.
- ROYLE, J. A., AND D. R. RUBENSTEIN. 2004. The role of species abundance in determining breeding origins of migratory birds with stable isotopes. *Ecological Applications* 14:1780–1788.
- RUBENSTEIN, D. R., C. P. CHAMBERLAIN, R. T. HOLMES, M. P. AYRES, J. R. WALDBAUER, G. R. GRAVES, AND N. C. TUROSS. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science* 295: 1062–1065.
- RUBENSTEIN, D. R., AND K. A. HOBSON. 2004. From birds to butterflies: Animal movement patterns and stable isotopes. *Trends in Ecology and Evolution* 19:256–263.
- RUEGG, K. C., AND T. B. SMITH. 2002. Not as the crow flies: A historical explanation for circuitous migration in Swainson's Thrush (*Catharus ustulatus*). *Proceedings of the Royal Society of London, Series B* 269:1375–1381.
- SALOMONSEN, F. 1955. The evolutionary significance of bird migration. *Biologiske Meddelelser* 22: 1–62.
- SHERRY, T. W., AND R. T. HOLMES. 1995. Summer versus winter limitation of populations: What are the issues and what is the evidence? Pages 85–120 *in* Ecology and Management of Neotropical Migratory Birds (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.

- SMITH, K. G. 2006. 100 Years Ago in the American Ornithologists' Union. *Auk* 123:924–925.
- SMITH, R. B., T. D. MEEHAN, AND B. O. WOLF. 2003. Assessing migration patterns of Sharp-shinned Hawks *Accipiter striatus* using stable-isotope and band encounter analysis. *Journal of Avian Biology* 34:387–392.
- SMITH, T. B., S. M. CLEGG, M. KIMURA, K. C. RUEGG, B. MILÁ, AND I. J. LOVETTE. 2005. Molecular genetic approaches to linking breeding and overwintering areas in five Neotropical migrant passerines. Pages 222–234 in *Birds of Two Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.
- SWARTH, H. W. 1920. Revision of the avian genus *Passerella*, with special reference to the distribution and migration of the races in California. University of California Publications in Zoology, no. 21.
- SZÉP, T., A. P. MØLLER, J. VALLNER, B. KOVÁCS, 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.
- VOELKER, G., AND S. ROHWER. 1998. Contrasts in scheduling of molt and migration in eastern and western warbling-vireos. *Auk* 115:142–155.
- WASSENAAR, L. I., AND K. A. HOBSON. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environmental Science and Technology* 35:1845–1850.
- WEBSTER, M. S., AND P. P. MARRA. 2005. The importance of understanding migratory connectivity and seasonal interactions. Pages 199–209 in *Birds of Two Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P. P. Marra, Eds.). 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.
- WECKSTEIN, J. D., D. E. KROODSMA, AND R. C. FAUCETT. 2002. Fox Sparrow (*Passerella iliaca*). In *The Birds of North America*, no. 715 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- WENINK, P. W., AND A. J. BAKER. 1996. Mitochondrial DNA lineages in composite flocks of migratory and wintering Dunlins (*Calidris alpina*). *Auk* 113:744–756.
- WENNERBERG, L. 2001. Breeding origin and migration pattern of Dunlin (*Calidris alpina*) revealed by mitochondrial DNA analysis. *Molecular Ecology* 10:1111–1120.
- WUNDER, M. B., C. L. KESTER, F. L. KNOPF, AND R. O. RYE. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia* 144:607–617.