Perspectives on Migratory Connectivity

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CHAPTER 3

PERSPECTIVES ON MIGRATORY CONNECTIVITY

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Abstract.—The previous two chapters present detailed case studies describing the connectivity in two Nearctic–Neotropical migratory songbirds, the American Redstart (*Setophaga ruticilla*) and the northern yellow warbler (*Dendroica petechia*; group *aestiva*). Using different approaches, these studies demonstrate how multiple sources of information and assignment techniques can be combined to reveal broad patterns of connectivity between breeding, wintering, and migration periods. Here, we summarize the results of these studies and briefly discuss whether these tools can be applied to other systems. We also explicitly address the assumptions, limitations, and potential sources of variation in these approaches. Next, we discuss how patterns of connectivity can be used to advance our understanding of population dynamics and make sound conservation decisions. Finally, we outline a few key ideas for future projects that we believe would make significant contributions to improving our ability to link migratory populations, placing emphasis on projects that would be suitable for graduate students interested in pursuing research in this field.

Resumen.—Los dos capítulos anteriores presentan casos detallados que describen la conexión Neártica-Neotropical de dos especies migratorias de aves canoras, *Setophaga ruticilla* y *Dendroica petechia*; grupo *aestiva*). Mediante el uso de diferentes análisis, estos estudios demostraron como múltiples fuentes de información y técnicas de asignación pueden se combinadas para demostrar patrones generales de conexión entre los sitios de reproducción, de invernada y los períodos de migración. En este capitulo, resumimos los resultados de estos estudios y discutimos brevemente si estas herramientas pueden ser utilizadas en otros sistemas. También nos referimos ampliamente a las suposiciones, limitaciones y a las fuentes potenciales de error en estos análisis. Acto seguido, discutimos como los patrones de conexión pueden ser usados para mejorar nuestro entendimiento sobre dinámica poblacional y tomar decisiones responsables sobre conservación. Por ultimo, hacemos énfasis en algunas ideas clave para los proyectos futuros que creemos harán contribuciones importantes para el mejoramiento de nuestra habilidad de enlazar las poblaciones de aves migratorias, poniendo énfasis en proyectos que creemos serian apropiados para estudiantes de postgrado interesados en este campo de investigación.

Describing migration patterns for birds has a long history (see Alerstam 1990, 2006), but the more recent applications of intrinsic markers, such as stable isotopes and genetic markers, have dramatically improved our ability to track the long-distance movements of birds. These technological advances have helped invigorate the study of migration and seasonal connectivity patterns (Webster et al. 2002, Webster and Marra 2005, Marra et al. 2006). Several studies over the past decade have used stable isotopes and molecular markers to examine migratory connectivity in a variety of species, such as raptors, waders, thrushes, and warblers (see Boulet and Norris [2006] for a partial list). Here, we summarize the major findings of the two studies presented in this monograph (Boulet et al. 2006, Norris et al. 2006), discuss limitations and advantages of the approaches, and address specific needs for future research in this field.

This monograph presents case studies that use intrinsic markers to study migratory connectivity of two songbirds, the American Redstart (*Setophaga ruticilla*; Norris et al. 2006) and the northern yellow warbler (*Dendroica petechia*;

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group *aestiva;* Boulet et al. 2006). Both of these species are small-bodied (<10 g), open-cup nesting, Nearctic–Neotropical migratory passerines that have relatively large geographic ranges. The American Redstart breeds in Canada and in the eastern United States and winters in Mexico, Central America, northern South America, Bermuda, and throughout the West Indies (Dunn and Garrett 1997; fig. 1B in Norris et al. 2006). The northern yellow warbler breeds across Canada, the United States, and northern Mexico and winters in Mexico, Central America, and northern South America (Dunn and Garrett 1997; appendix 1 in Boulet et al. 2006). As with most migratory songbirds, the patterns of connectivity for these species have been only marginally understood. This is largely because of the logistic difficulties associated with use of more conventional extrinsic markers, such as band recoveries, to track birds between different periods of the year. The large spatial extent of the ranges used by these species, coupled with the relative paucity of targeted field effort, means that birds marked in one season are rarely recaptured or seen at disparate locations during other periods of the annual cycle. The use of intrinsic markers has helped increase the efficiency of field efforts because the origin of every individual captured can be estimated.

Both studies rely on latitudinal variation of δD in precipitation in North America to help infer the breeding origin of individuals sampled in previous seasons. Each study uses additional information with δD in feathers to better resolve spatial connections. Norris et al. (2006) combined modeled precipitation-based δD values (Bowen et al. 2005) with estimates of relative breeding abundance from the Breeding Bird Survey (BBS; Sauer et al. 2004) to refine regional assignment probabilities for five non-overlapping breeding origins, which were then used to estimate the breeding origin of birds sampled during winter. Boulet et al. (2006) used the same model-based precipitation δD values to restrict the spatial extent of regional assignment probabilities for breeding origins initially based on a genetic marker (mitochondrial DNA [mtDNA]) and band-recovery data. This iterative method was used to estimate the breeding origin of birds sampled during migration and in winter.

Results from Norris et al. (2006) suggest a broad pattern of parallel migration between breeding and wintering populations of American Redstarts, whereby birds wintering in Mexico and Central America were most likely to have bred in north and central North America and birds wintering in the Greater and Lesser Antilles were more likely to have bred in eastern North America. In addition, within a portion of the wintering range, δD values in feathers, presumed to have grown on the breeding grounds, were highly correlated with the sampling latitude during winter. This suggests a pattern of chain migration, whereby individuals wintering at northernmost latitudes had the highest probability of breeding at relatively more northern latitudes and more southerly wintering birds were most likely to have bred farther south.

Boulet et al. (2006) found that eastern and western genetic lineages segregated throughout the annual cycle, with some overlap of lineages in central North America during the breeding season (Boulet et al. 2006). These results suggest a parallel migration system with strong connectivity between eastern North America and Venezuela, and between western North America and Mexico. Adding isotope markers as a further geographic discriminator within each lineage revealed weak connectivity between some regions. By considering band-return data in addition to these results, Boulet et al. (2006) were able to converge on a more refined sense of possible migratory routes taken by eastern and western populations.

Overall, these studies show how multiple sources of information and assignment techniques can be used to describe general patterns of connectivity in widely distributed species. In the following sections, we briefly describe the extent to which these tools can be applied to other systems in the context of a discussion of notable limitations, assumptions, and potential sources of variation. We then ask how information on connectivity can inform population models and conservation decisions. Using these case studies as learning tools, our primary goal is to provide some insight for future projects aimed at improving our ability to link migratory populations between different periods of the annual cycle.

Generality of Approach and Key Assumptions

The case studies presented in this volume illustrate two related but different approaches that combine intrinsic markers and additional information to study migratory connectivity. Here, we consider the natural history of these species and some of the assumptions associated with these approaches. In doing so, we highlight aspects of these studies that can be generalized to other systems and note others that may be limiting.

The two species in this monograph not only have broad geographic ranges, as noted above, but they are also relatively common (Sauer et al. 2004). These characteristics bear directly on the availability of different types of data to study connectivity. First, common species will have a higher probability of being captured and recaptured at banding stations than a rare species (with a similar geographic range). Band-recovery data, therefore, are more extensive and informative for species with overall higher densities. Given similar field-effort levels, encounter rates and, therefore, band-recovery rates can also be relatively high for species with restricted geographic ranges (even if they are rare). However, even in species that occur at high densities, recapture probabilities between different seasons are still rather low (typically <0.5% for small songbirds; Brewer et al. 2000, Bairlein 2001) and become even lower when recaptures that occur between alternate stationary (nonmigratory) periods are considered. In the studies reported in this monograph, for example, there were 8 band recoveries between the stationary breeding and wintering periods for American Redstarts over a 79-year period (Norris et al. 2006) and 57 recoveries between breeding, wintering, and migration periods for northern yellow warblers over an 82-year period (Boulet et al. 2006). This information provided a very general picture of migration pathways for these species but was insufficient to make inferences about the overall degree of connectivity. Clearly, band-recovery data will be unavailable or sparse for many species. However, we emphasize that this is still the most spatially accurate information on migration movements and is valuable when used in conjunction with other information, such as intrinsic markers.

Relative abundance can inform spatially defined assignment probabilities (Royle and Rubenstein 2004, Marra et al. 2006). In this monograph, Norris et al. (2006) used relative abundances estimated from BBS data to inform the estimated probabilities for the potential breeding origins. Wintering individuals were considered, *a priori*, to have a higher probability of originating from breeding regions with higher relative densities. The effective use of relative abundance to estimate connectivity in this way is limited to those species that are well sampled across their range (i.e., well distributed within the range covered by the BBS or a similar range-wide systematic survey effort). More importantly, however, the use of survey-based relative abundances rests firmly on the assumption that the survey results are representative of the true relative abundances. For example, the BBS is limited to sampling birds along roads, and not all species are well represented by such roadside surveys. Even for those that are, the added assumption of even detection probability over time and space is questionable (Williams et al. 2002). Nevertheless, the use of relative abundance can be helpful when the data are relatively consistent between the areas of interest, and even more so when the abundance estimates vary widely between predefined potential areas of origin.

The large geographic extent of the breeding ranges of the two species studied means that they also encompass a wide range of modeled δD values for precipitation across North America. This increases the likelihood that differences in δD values of feathers will be detected over broad latitudinal gradients.

The use of δD values in feathers to estimate the origin of birds using modeled δD in precipitation depends on a number of largely untested key assumptions. First, all studies thus far that have used interpolated maps of δD in precipitation, including the two presented in this monograph, have not considered any process error in the foundational model. That is, they depend on expected δD values from a spatially interpolated time-averaged model of δD in precipitation (Hobson and Wassenaar 1997, Bowen et al. 2005). Once these mean values are extracted, variance derived from spatial interpolation of δD is typically dropped (e.g., Hobson and Wassenaar 1997, Wassenaar and Hobson 2001, Norris et al. 2004), despite the fact that this variance can range from 2‰ to 40‰ (Bowen et al. 2005). The inferential effects of considering this model-derived variance have not been explored, and temporal variance has also not been estimated for any of the interpolation models.

A second fundamental and largely untested assumption is the statistical representation of isotopic values within a region. In some cases, this has been represented by a single value. In more recent cases, geographic regions have been represented by a probability distribution of isotope values using either feathers of known origin (Caccamise et al. 2000, Wassenaar and Hobson 2000, Kelly et al. 2005, Wunder et al. 2005) or modeled values based on precipitation (Royle and Rubenstein 2004, Boulet et al. 2006, Norris et al. 2006). The use of probability distribution is preferable, but studies that have done so have assumed a normal distribution, which remains largely untested.

A third assumption is that mean precipitation values are linearly and uniformly related to feather values. Most studies thus far use a fixed discrimination factor between δD in precipitation and δD in feathers (or other tissue). Although there is general support for this assumption, discrimination values vary between and within studies (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Wassenaar and Hobson 2000, Bowen et al. 2005, Lott and Smith 2006). We have only begun to fully explore deviations from this expectation (Hobson 2005). Age of the bird can influence the δD values observed in feathers (Meehan et al. 2003). McKechnie et al. (2004) report experimental results that heat stress can strongly influence the turnover rates and incorporation of δD in body water. Birchall et al. (2005) suggest that trophic level may influence observed δD values. Wunder et al. (2005) report wide ranges of δD from single sites, years, and age classes, which suggests that variation in diet source can be wide, especially for opportunistic foraging species.

Finally, a specific season of growth is usually assumed for feathers used in stable isotope analyses. Both Norris et al. (2006) and Boulet et al. (2006) sampled tail feathers to estimate the breeding origin of American Redstarts and northern yellow warblers sampled during the nonbreeding period. However, from a breeding site in Ontario, Norris et al. (2004) recaptured marked American Redstarts that were known to have bred at the same location the previous season. Analysis of δD in tail feathers suggested that some individuals may have molted their feathers during fall migration and not on the breeding grounds as previously assumed. More recent analysis of δD in primary flight feathers of returning American Redstarts suggests that these feather types are consistently molted on the breeding grounds before fall migration and will probably provide a more accurate estimate of breeding origin than tail feathers (D. R. Norris, M. W. Reudink and K. L. Langin, unpubl. data). Thus, the use of known-origin birds may be required to examine which feathers are consistently molted during any period of interest. A strong working knowledge of the timing of molt is critical to the effective use of isotopes in feathers.

The use of δD to study migratory connectivity remains very promising, but we agree with Hobson (2005) that there remains a lot of room for refinement. The increasing use of δD in studies of migratory connectivity will undoubtedly produce results that yield surprising patterns. It is the unexpected results that will advance our understanding of migratory ecology and conservation, and we encourage the publication of such studies. However, we also emphasize that more experimental work is needed to test assumptions about the factors contributing to these potential sources of variation in isotope values.

Genetic markers have fundamentally different properties than stable-isotope markers: they are inherited from maternal line (mtDNA, W chromosome in birds), paternal line (Y chromosome in mammals), or biparental lines (nuclear markers not located on sexual chromosomes). Thus, genetic markers are fixed at birth and are directly linked with population structure and evolution (Avise 2004). Stable isotopes, by contrast, are acquired from the environment and integrated into growing tissues, many of which remain metabolically active and, therefore, show constant turnover of elements (Hobson 1999). These differences can produce discordant outcomes when they are used as markers to trace animal movements. Although stable isotopes may estimate where a specific tissue was produced, genetic markers estimate where an individual was born. For example, if a hatch-year bird or a philopatric after-hatch-year bird produced its flight feathers on the natal grounds, stable-isotope and genetic markers will produce concordant results. However, if a bird disperses to new breeding area and grows feathers at that new location, genetic markers will not be able to estimate the true breeding origin of that individual from the previous season. However, discordant results between markers can be useful for other purposes, such as estimating rates of long-distance dispersal between breeding seasons.

Clearly, genetic markers are useful for assessing migratory connectivity only if significant genetic differentiation exists between populations. Thus, the use of genetic markers is linked to the evolutionary history of the species and levels of gene flow between populations. In the Northern Hemisphere, the Pleistocene glaciations, which repeatedly occurred over the past 700,000 years, are considered important isolating agents for avian populations (Avise and Walker 1998, Avise et al. 1998, Johnson and Cicero 2004). These glaciation cycles have likely played a major role in speciation, the emergence of subspecies, and, in the case of the last two glaciation events, producing significant patterns of population structure in many taxa (Holder et al. 1999, Milot et al. 2000, Ruegg and Smith 2002, Johnson and Cicero 2004, Boulet and Gibbs 2006). This is because many avian populations were isolated in distinct refugia and subsequently underwent genetic differentiation (Bermingham et al. 1992, Holder et al. 1999). Other isolating agents, such as large geographic distances between populations (i.e., isolation by distance), bottlenecks, founder effects, and geographic barriers such as mountains, water bodies, islands, and deserts (Zink 1997, Avise 2000), can create significant patterns of population structure in avian species. However, concordant large-scale patterns of population structure have been observed in a number of Nearctic–Neotropical migratory birds, which suggests that Pleistocene glaciations have played a primary role in the evolutionary history of these species (Kimura et al. 2002, Ruegg and Smith 2002, Lovette et al. 2004, Boulet and Gibbs 2006).

These observations suggest that populations that were isolated in distinct refugia during the last glaciation cycles will likely show sufficient genetic differentiation to allow development of genetic markers. So far, the best genetic marker for detecting large-scale patterns is mtDNA. At the continental scale, mtDNA markers are suitable for species that have a very large longitudinal distribution and share a evolutionary history, such as Swainson's Thrush (*Catharus ustulatus*), Wilson's Warbler (*Wilsonia pusilla*), and northern yellow warbler, where strong east–west genetic differentiation has been observed (Kimura et al. 2002, Ruegg and Smith 2002, Boulet and Gibbs 2006). In species with smaller breeding ranges that were isolated in a single refugium, mtDNA may not provide sufficient levels of differentiation for assessment of migratory connectivity (Davis et al. 2006). For taxa with limited ranges, multilocus markers, such as microsatellite and amplified fragment-length polymorphism (AFLP), may show more promise.

USING INFORMATION ON MIGRATORY CONNECTIVITY

Describing patterns of migratory connectivity is critical for improving our understanding of the ecology of migratory birds (Webster et al. 2002, Webster and Marra 2005, Marra et al. 2006). As the two studies in this monograph illustrate, we are beginning to gain a more complete picture of migration patterns and connectivity between periods of the annual cycle in some species. As we more thoroughly test the assumptions underlying the use of intrinsic markers, we believe it is also important to consider potential applications of this information.

Determining the factors that limit and regulate avian populations requires an understanding of how events interact between periods of the annual cycle (Sherry and Holmes 1995, Marra et al. 1998). Current and future studies on connectivity can help elucidate how events between seasons interact to influence both population-level effects, such as survival and fecundity, and individual-level effects, such as breeding or social status (Webster and Marra 2005). If, for example, strong connectivity exists between two populations, then events such as habitat loss and annual variation in climate in one season can be correlated with population- and individual-level effects the following season. For example, using stable isotopes, Chamberlain et al. (1997) and later Rubenstein et al. (2002) suggested that northern breeding populations of Black-throated Blue Warblers (*Dendroica caerulescens*) in eastern North America primarily winter in Jamaica and Cuba, whereas southern breeding populations primarily winter in Puerto Rico and Hispaniola. Building on this information, Sillett et al. (2000) found that annual fecundity in a northern breeding population of Black-throated Blue Warblers in New Hampshire was correlated with the number of juveniles found the following year in Jamaica.

In contrast to strong connectivity, recent models suggest that when populations are mixed between the breeding and wintering grounds, events (such as habitat loss) in one season will influence population size over a wide geographic area (Marra et al. 2006). Information on connectivity coupled with estimates of habitat loss and population metrics can be used to test this prediction.

Another field where information on migratory connectivity will be useful is conservation planning. Allocating resources and prioritizing decisions to conserve habitats (e.g., Wilson et al. 2006) in migratory animals will partly depend on how populations are spatially connected between periods of the annual cycle. As an example, consider a migratory species that breeds in a threatened habitat in North America and winters throughout South America. Assume that our goals are to avoid local extinctions of breeding populations and maintain the size of the breeding range. To accomplish this goal, we have a limited amount of funding to establish reserves. Focusing on the breeding grounds may initially be effective at maintaining breeding populations but may only increase population size until the species is limited by habitat availability on the wintering grounds. Conserving breeding populations, therefore, will depend partly on establishing reserves during the wintering period as well. Decisions on how to design networks of reserves on the wintering grounds, however, will depend on the spatial patterns of connections between the breeding and wintering ranges. For example, if breeding populations completely mix on the wintering grounds, reserves might be placed evenly throughout the wintering range. However, if specific breeding populations of interest show strong connectivity to specific wintering areas, conserving nonbreeding habitats used by these populations will become one of the priorities in designing a reserve network to maintain breeding populations. For migratory animals, models designed to optimize the allocation of finite resources, therefore, would strongly benefit from explicitly considering patterns of connectivity between seasons.

The fields of population ecology and conservation biology arguably stand to benefit the most from a better understanding of migratory connectivity. Building on current studies of connectivity and testing their assumptions will, therefore, provide valuable information in these fields.

Future Studies

In the previous sections, we highlighted several issues related to measuring migratory connectivity and how connectivity can be used to understand migratory ecology. Following these discussions, we will now briefly outline a few key ideas for future projects that we believe would make significant contributions to improving our ability to link migratory populations. We place particular emphasis on projects we believe would be suitable for graduate students interested in pursuing research in this field.

Molt ecology using stable isotopes.—Feathers are useful for tracking the movement of birds using stable isotopes and trace elements because they are metabolically inert after growth and, therefore, provide an elemental signature of the location where they were grown. Additionally, sampling feathers is relatively non-invasive. Understanding the variation in molt schedules between feather types, individuals, and populations will be essential for interpreting results from chemical markers. In the use of stable isotopes to study patterns and timing of molt, it is important to use feathers of known origin in conjunction with individuals of known origin. In this way, expected distributions of isotope values from freshly molted feathers are coupled with feathers that are assumed to have been grown at the same time from an individual recaptured at a different time. Better understanding of the resolution with which we can use isotopes to infer molt ecology will help gauge the extent to which we can use alternate methods to study life-history tradeoffs between the timing and location of molt, reproduction, migration, and development of sexually selected feather signals.

Additional genetic markers to increase the resolution of population structure.—Assessment of migratory connectivity by way of genetic markers primarily relies on our ability to detect significant levels of genetic structure between breeding populations. We need to develop additional markers that will provide enough resolution to verify the presence of genetic structure and increase the ability to detect patterns of connectivity, particularly in species with relatively small breeding ranges (e.g., ranges limited to eastern or western North America). This will require genotyping individuals at numerous polymorphic nuclear loci to increase the statistical power to detect significant genetic structure among breeding populations and to be able to use population assignment tests to estimate the origin of individuals. So far, most avian studies have relied on a small number of microsatellite markers (<10 loci) and have found only limited levels of genetic differentiation with these markers (Gibbs et al. 2000, Bulgin et al. 2003, Clegg et al. 2003, Davis et al. 2006). Amplified fragment-length polymorphisms may show more promise, because they can generate a higher number of loci without intensive species-specific development of markers (e.g., Busch et al. 2000, Wang et al. 2003, Boulet et al. 2005).

Comprehensive genetic sampling.—Migratory connectivity studies that include genetic markers are usually geographically incomplete: some areas of the annual distribution are usually poorly sampled or not sampled at all. Additional studies are required to better delineate distributions of divergent populations in each of the key habitats used by migrants during the annual cycle. In the northern yellow warbler, for example, additional sampling across a wider geographic area would help delineate the annual distributions of each lineage, particularly on the wintering grounds (Boulet et al. 2006). At a finer scale, the zone of introgression between lineages also needs to be more thoroughly described, including verifying how stable zones are over multiple years. Collaboration among researchers to sample across the entire geographic range of a species will be essential for advancing the field (Smith et al. 2003). Collaborative research networks will be especially important in species with annual distributions that span several countries.

Statistical methods.—Improving the understanding of connectivity will require novel and varied statistical techniques. One of the first challenges will be to combine data of different types (e.g., continuous and categorical) in a single probability-based framework. An even bigger challenge, however, will be to develop methods that can integrate both empirical and model-based information to help probabilistically characterize areas that are not directly sampled. We strongly advise grounding all exploration in probability theory, and not limiting work to current linear-model frameworks.

Factors influencing the diet–tissue discrimination factor in stable isotopes.—Experiments are still needed to quantify the extent to which isotopes are conserved along typical metabolic pathways. This work is needed to improve interpretations of isotope values observed in the field. This may be done best at the compound level, but certainly some insight can still be gained from tissue-level studies.

Spatial variation of stable isotopes in avian tissues.—We still have a relatively poor understanding of how various isotopes vary in avian tissues across broad geographic regions. A coordinated sampling effort is required to map isotopic variation in tissue at differing spatial resolutions and to understand how values vary according to climatic, biological, and geological processes. This effort should be focused not only on improving our knowledge of the frequently used light isotopes (δD, $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) but also on developing basemaps of heavier isotopes, such as strontium, lead, and calcium.

Temporal variation of stable isotopes in avian tissues.—We also have a relatively poor understanding of the extent to which spatially local isotope values fluctuate with time. If there are deterministic fluctuations in isotope values with time, we can use that source of variance to refine isotope-based inferences.

Connectivity and population dynamics.—As information on connectivity improves, there will be important opportunities to examine how regional population dynamics are linked to phenomena such as climate variation or habitat loss in previous periods of the annual cycle. Separating the components that are driving population variation on the basis of the degree of connectivity between different periods will provide valuable insight into how and when populations are limited. Previous simulation models can form the basis for generating specific predictions about how populations should respond to habitat loss or climate change depending on the degree of connectivity between periods (Dolman and Sutherland 1995, Marra et al. 2006).

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