Forging New LINKS in Bird Migration

Across the continent each spring, everyday people await the return of migratory birds to their back yards, city parks, and other familiar places. It seems it is never truly spring until the Yellow Warbler is again singing its song from the dogwood, until a sudden flash of orange reminds you of the orioles that nested down by the river last year, or until you can't resist taking a closer look at a high soaring bird in hope that the Swainson's Hawks have again returned from Argentina. The natural beauty of migratory birds is a source of delight for millions of enthusiasts who throng outdoors each spring to catch the spectacle of avian diversity.

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However, in recent decades, birders and biologists alike have noticed declining numbers of many migratory species that breed in North America but spend the non-breeding season in Central or South America. There are increasing concerns about the effects of local, regional, and global changes on habitats for these species. In contrast to resident species, understanding the factors that govern population sizes of migratory birds requires a grasp of the geographic range and habitat requirements in both breeding and non-breeding areas, which may be many thousands of miles apart.

Biologists have traditionally used leg bands for tracking the paths of migrating birds, but for non-game species, banding has yielded relatively little information about their seasonal movements. Only about 0.05% of birds banded are ever recaptured, and the sheer number of individuals of any one species makes the possibility of re-sighting most color-banded birds on their non-breeding grounds highly unlikely. More recently, improvements in technology have made it possible to mount radio or satellite transmitters on migrating birds. However, these techniques also have their limitations. Satellite transmitters are heavy and can be used only on large birds, while radio transmitters, though light enough to be mounted on even very small birds, have a very limited range and battery life. And while these techniques have provided many clues to the migratory mystery, what they have largely failed to provide is an understanding of how *individual* birds move between their summer and winter habitats. But biologists now have an amazing new tool in their hands—stable isotope analysis—that is helping to tie together the lives of migratory birds.

What is Stable Isotope Analysis?

The saying "you are what you eat" has taken on new meaning since the discovery that certain chemical elements in animal tissues are linked to diet. Certain atoms of an element may have a different weight than others. These are known as isotopes of that element. Deuterium, for example, is a stable isotope of hydrogen that has an extra neutron, making it heavier than a "normal" hydrogen atom, which lacks the extra neutron.

Deuterium occurs naturally in rainwater and enters the food chain through the tissues of plants. Interestingly, concentrations of deuterium vary predictably across the continent, with lower amounts occurring in northwestern regions of North America and higher amounts in southeastern regions. The reasons for this pattern are complex, but they are basically due to continent-wide differences in precipitation, which in turn result in differences in the amount of deuterium falling to the earth as rain or snow. Also, because there is more precipitation near the equator and less near the poles, ratios of the hydrogen isotopes vary by latitude. In general, less deuterium is found in precipitation farther away from the equator (Hobson and Wassenaar 1997; see Fig. 1). Proportions of stable isotopes of other elements, including carbon, sulfur, and strontium, also vary across the global landscape in predictable ways.

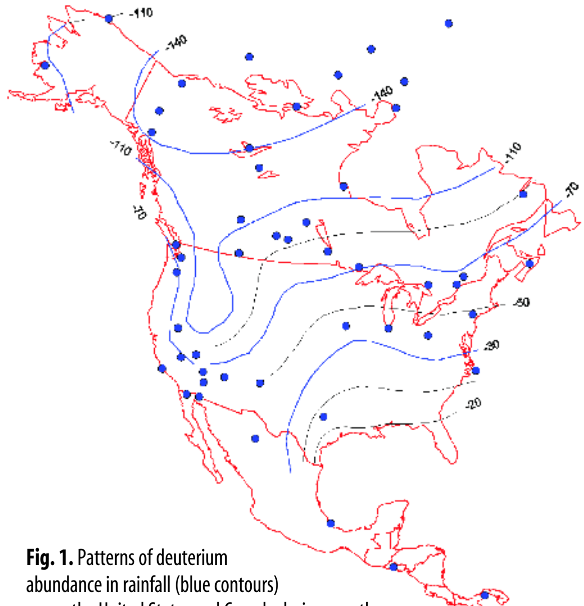
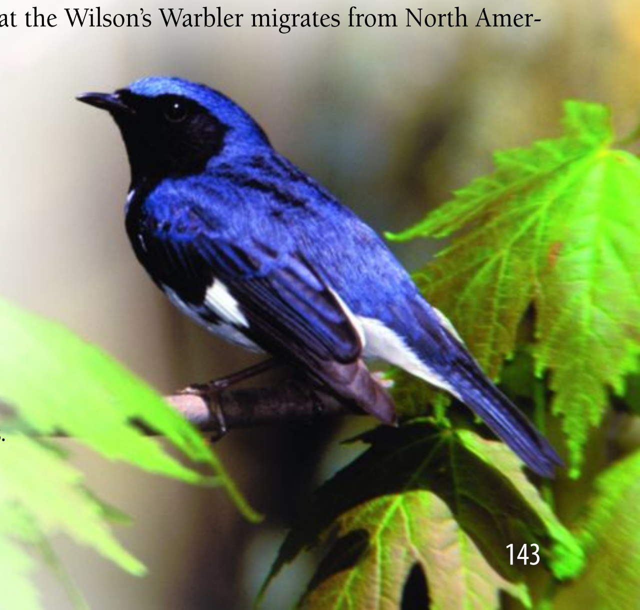


Fig. 1. Patterns of deuterium abundance in rainfall (blue contours) across the United States and Canada during months when the average temperature exceeded 0° C. Dots represent Global Network for Isotopes in Precipitation (GNIP) monitoring sites. *Figure reproduced from Hobson and Wassenaar (1997) with permission.*

When an animal ingests water and food, its body tissues absorb the isotopes and take on chemical "signatures" of the geographic area where it resides. The turnover rate of the isotopes differs among tissues. For example, carbon isotopes have a turnover rate of a few days in liver tissue, a few weeks in muscle and blood, and up to six months in bone collagen. As a result, a bird that migrates across geologic areas with large isotopic gradients or different ecological biomes, such as North America, will exhibit different isotopic concentrations in its various body tissues.

But feathers are unique, relative to other body tissues, in that they grow in a very short time and then become metabolically inert. Consequently, the isotopic content of a feather will reflect the bird's diet during the short time in which the feather was grown, and, more importantly, the area where the feather developed. And so feathers sampled from young-of-the-year as they migrate southward will indicate breeding-ground location, while those taken from after-second-year adults heading north will indicate their molting region from the previous year. Because biologists can precisely measure chemical concentrations with a machine called a mass spectrometer, natural variations in the stable isotopic composition in bird feathers can therefore be used to delineate their geographic origin. The spatial resolution of this technique is still relatively low. Researchers may be able to place the growth origin of a feather to within only 30° latitude within continental North America (e.g., Kelly et al. 2002). In the future, however, combining information from several stable isotopes, together with better mapping of the distribution of stable isotope ratios across broad geographic areas, will allow biologists to pinpoint more closely the geographic location where the feathers were grown.

In this way, researchers at Dartmouth University analyzed the migration patterns of the Black-throated Blue Warbler, using the natural patterns of abundance of deuterium and carbon-13 in the environment. They uncovered the surprising existence of two separate populations with drastically different migration routes. Warblers breeding in the northern United States appear to migrate to the western Caribbean, while those breeding in the southern United States migrate to the eastern Caribbean (Rubenstein et al. 2002). Another study has revealed an unexpected pattern of migration in an otherwise well-known species. Use of stable isotopes has shown that the Wilson's Warbler migrates from North Amer-



Migratory birds carry natural geographic "signatures"—the isotopes contained in their feathers. And by analyzing the stable isotope composition of birds' feathers, researchers are learning surprising things about the distribution, movements, and population health of many species. Work with the Black-throated Blue Warbler (shown here), for example, has demonstrated the existence of two separate populations with dramatically different wintering, breeding, and migratory distributions. *Point Pelee, Ontario; May 1999. © Arthur Morris / Birds As Art.*

ica to Central America in a leapfrog pattern. In other words, individuals breeding in the most northerly part of their North American range actually migrate over more southerly breeders to winter on the southern edge of the species' non-breeding range (Kelly et al. 2002).

Stable isotope analysis has also become extremely useful in determining the molting and breeding origins of seabirds. Due to temporal and spatial segregation between breeding and molting areas in most seabirds, our knowledge of their food and feeding ecology has mainly been restricted to the breeding season, when they are accessible in colonies. As a result, little is known about where most seabirds spend weeks and months at sea between breeding events. The Black-browed Albatross, for example, ranges over enormous stretches of open ocean after breeding, but the food sources and foraging locations important to non-breeding birds are unknown. In this case, stable isotope analysis of feather samples together with limited band recoveries has provided evidence that this species winters in the subtropical waters of southern Australia and feeds far offshore (Cherel et al. 2000).

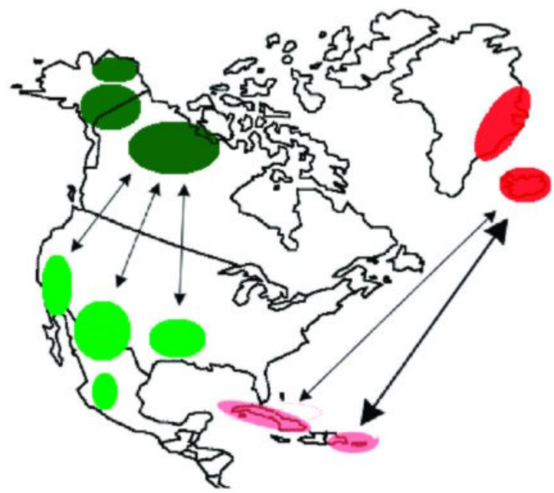


Fig. 2. The strength of migratory connectivity. Populations of many migratory species may exist as more-or-less distinct subpopulations. This figure represents breeding sub-ranges (dark shades) and wintering sub-ranges (light shades) of two hypothetical migratory bird species (green and red). Populations in the breeding range are connected to those in the non-breeding range by the migration of individuals. **Strong connectivity** exists when most individuals from one breeding population (red) move to the same non-breeding location (pink) to form a non-breeding population with a relatively small proportion of individuals migrating to other winter locations (thin arrows). **Weak connectivity** exists when individuals from a single breeding population (dark green) migrate to several different overwintering locations spread throughout the non-breeding range (light green). *Adapted from Webster et al. (2002).*

Stable isotope analysis can also help answer other types of questions about migratory birds. Due to the short summers at high latitudes, arctic migrants have been presumed to bring nutrients for egg production from their previous habitats so that they can start breeding immediately upon arrival. To test this hypothesis, Klaassen et al. (2001) took advantage of the different diets of wintering and migratory vs. breeding shorebirds. During winter and migration, most arctic-breeding shorebirds eat estuarine invertebrates; but they shift to terrestrial invertebrates, which have distinctly different carbon-isotope ratios, on their tundra breeding grounds (Peterson and Fry 1987). Diet-based differences in carbon-isotope ratios are expressed in bird tissues, including eggs. In this way, researchers could determine if the carbon ratios of eggs matched those of migratory or breeding habitat and, therefore, determine where the nutrients that produced the eggs came from. Results showed that all ten species of shorebirds investigated produced eggs using local nutrient sources. For these waders, the cost of transporting extra nutrient stores to the breeding grounds evidently outweighed the benefits (Klaassen et al. 2001).

Obtaining this kind of detailed information using band-recovery or through radio-telemetry would be extremely expensive and time-consuming, if not impossible. The new technique has also proven relatively inexpensive and has little impact upon the birds that are sampled. In contrast to traditional mark-and-recapture methods, using stable isotope analysis requires only a knowledge of the distribution of isotope abundance across the geographic range of the bird and is relatively non-invasive, requiring only a feather sample.

A Tool for Conservation

One of the greatest difficulties in effectively managing populations of neotropical migratory birds is the general inability to link events on the wintering grounds with subsequent events on the breeding grounds when these birds return to North America (Hobson 1999). Two of the most important factors contributing to reproductive success among songbirds are date of arrival and commencement of nesting. Individuals able to breed earlier are often more successful than late breeders.

Marra et al. (1998) gained insight into the mechanisms controlling the arrival date of American Redstarts in North America by comparing their tissue carbon-12/carbon-13 ratios. Redstarts wintering in moist Jamaican forests had depleted carbon-13 values compared with those inhabiting poorer-quality, second-growth scrub habitat. These isotopic differences were based on the relative abundance of C3 vs. C4 plants between these two habitats. Hotter, drier areas typically have more C4 plants, which are better able to conserve water, and which have enriched carbon-13 values compared with C3 plants (Lajtha and Marshall 1994). Marra et al. (1998) found that American Redstarts occupying dry, secondary habitats were in worse condition than those in forest habitats, and they predicted that these would be the individuals to arrive later on the breeding grounds. Their conclusion—namely, that winter habitats are limiting for redstarts—has important conservation implications for the long-term stability of migratory bird populations, many of which are declining and of conservation concern (Marra et al. 1998). It also provided, for the first time, a means of understanding factors affecting breeding-ground performance in the past and at distant locations (Hobson 1999).

Thus, important connections exist between conditions in one season and performance in the next. But because populations may mix to different degrees during the breeding and non-breeding season, the strength of connectivity of populations between these habitats is also important in assessing threats and for designing recovery plans for declining species. Recent studies of migration patterns using stable isotopes are revealing previously unsuspected patterns of migration. Such results are making it increasingly obvious that efforts to maintain healthy populations of migratory birds will have to take these patterns into account, because species often differ in the migratory connectivity of their populations.

A species may be extremely vulnerable, for example, if large portions of its population migrate to a restricted wintering location, or vice versa. Such a species, having all its "eggs in one basket", is likely to be especially vulnerable to habitat destruction, global warming, hunting, or other impacts if there are no alternative habitats to choose from. A case in point is the endangered Kirtland's Warbler, which breeds in a very restricted area of northern Michigan and which winters on a few islands in the Bahamas. Both of these areas are crucial to the long-term population viability of the species. Because of its extremely restricted summer and winter ranges, Kirtland's Warbler is one of few species for which we generally know where most breeding individuals spend their summers and winters. However, in most migratory species, this is not the case.

Thus, determining the level of connectivity between the breeding and non-breeding locations (Fig. 2) will be an important step in assessing how local populations are affected by events in either the summer or winter. Some migratory species are undergoing consistent population declines in some regions and increases in others. This variability could be due to the fact that certain populations wintering or breeding in specific areas may be more affected by habitat loss or degradation than others. Understanding linkages between areas used by birds throughout their yearly cycle is then critical to their effective conservation, since efforts can be directed more appropriately at breeding, wintering, or stopover sites (Myers et al. 1987).

Stable isotope analysis has been successfully used to understand food-web structures in and between terrestrial and aquatic ecosystems (Tieszen and Boutton 1988), to track the breeding origin of anadromous fish to their natal streams (Kennedy et al. 1997), and to identify distinct populations of elephants (Vogel et al. 1990). Stable isotope analysis also can be used to follow the path of pollutants through ecosystems (Macko and Ostrom 1994). Even tissue samples taken in the past may also become useful. Because stable isotopes of different elements differ among food sources, biologists are currently using feathers from museum specimens to determine if long-term population declines in White-tailed Kite may be due to a change in diet.

The enormous potential of this technology to investigate the diets of organisms, migratory pathways, and even reproductive strategies and predator-prey relationships is largely untapped. Future research may be able to combine knowledge of the distribution of stable isotopes with genetic markers, providing even greater geographic resolution of feather origins, and establishing stronger linkages between migrating populations.

We are now on the verge of an explosion in the use of stable isotopes to answer a multitude of ecological questions and to explore more deeply the mystery of migration. Clearly, improved understanding of the ecology of migratory birds will only increase the effectiveness of efforts to protect the habitats that migrants depend upon throughout their yearly cycle and help ensure that the regular arrival of our avian neighbors will continue to brighten our familiar places.

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