Tracking migrant songbirds with stable isotopes

Migration is a fundamental aspect of avian biology and one of the most astounding phenomena in the natural world. In North America alone there are approximately 350 species of land birds that migrate seasonally. Most of these species weigh considerably less than 50 g and travel thousands of kilometers twice annually. Migratory biology has attracted and, in no small measure, frustrated generations of ornithologists. Much of the frustration can be traced to a simple source – namely, it is very difficult to study an individual migrating bird for any appreciable time or distance. Traditional tracking techniques, such as radio-telemetry and banding, are largely inadequate when applied to small birds that travel large distances in short time periods.

Our limited ability to trace migrant birds from breeding areas through migration to wintering areas and back again has left an astonishingly large gap in our knowledge of the biology of perhaps the best known taxon in the world. Recently, Hobson and Wassenaar[1] and Chamberlain *et al.*[2] have employed stable isotope analyses in a manner that promises to narrow this gap significantly. By improving our ability to link the breeding and wintering areas of migrant individuals these techniques have the potential to revolutionize our understanding of bird migration.

Isotopes in the environment

Natural variation in the occurrence of stable isotopes in the environment makes them useful for studying birds. Some of the more commonly studied isotopes have been those of carbon (C), nitrogen (N), and hydrogen (H). Studies of carbon isotope ratios have been valuable because the rate at which ^{13}C and ^{12}C isotopes are fixed by plants differs among photosynthetic pathways; C_4 plants have proportionally greater content of ^{13}C than do C_3 plants[3]. Because C_3 plants predominate at high latitudes and C_4 plants are more common at low latitudes, there is a latitudinal gradient in δ^{13}C (a standardized measure of the ^{13}C/^{12}C ratio) of plant communities[4]. Similarly δ^{15}N differs among terrestrial and marine plants; marine plants have higher values of δ^{15}N relative to terrestrial plants[5]. Finally, there is a latitudinal gradient in δD (deuterium) of growing-season rainfall; the relative occurrence of D decreases with increasing latitude[1,2]. The latitudinal pattern in δD is also evident in plants. The values of δ^{13}C, δ^{15}N, and δD in plants are transferred through the food webs that depend on them[4,5]. As a consequence of these patterns, stable isotopes can be used as naturally occurring markers to provide insights into the ecology of animals. In particular, analyses of δ^{13}C and δ^{15}N have provided numerous insights into the trophic ecology of birds (Box 1).

While the analyses of C and N isotopes have advanced our understanding of avian biology, their utility in studying migrant birds has been limited to those situations in which birds migrated from C_3 to C_4 or from terrestrial to marine systems. This limitation arises because the δ^{13}C and δ^{15}N values of animal tissues are primarily a result of diet rather than geographic location. So, these isotopes have limited capacity to act as general markers that link individual birds to geographic regions. δD values of tissues, however, are not diet-dependent, and therefore hydrogen isotopes have potential for use as a general geographic marker.

δD as a geographic marker

Before δD could be useful in studies of bird migration, three potential obstacles needed to be overcome. The first was finding a tissue that was renewed seasonally. That is, the δD values of whatever tissue was sampled would have to reflect only the δD signature of the breeding ground (or winter ground) and not an integration of the δD signature from breeding, wintering, and migration areas. So only tissues formed entirely within a season (i.e. in a single region) would be useful; for songbirds, the obvious tissue is feathers (Box 2). The second obstacle was ensuring that the δD values of this tissue represented a reliable record. This problem was potentially acute in feathers because 40% of the H contained in feathers is potential exchangeable with the environment[2]. To be a useful marker in migrating birds, the actual exchange of H between feathers and the surrounding environment would have to be low. Chamberlain *et al.*[2] provide the first evidence that the H isotopic ratios of feathers are largely fixed once they are fully formed (Box 2).

The third and final obstacle was documenting the relationship between the δD values of feathers and those values of precipitation in the region where the feathers were grown. To address this issue, Hobson and Wassenaar[1] used precipitation data from 40 locations throughout the USA and Canada to create a kriged continental-scale map with six isoclines of δD values. They then analyzed the δD values in feathers collected from six species of migrant insectivorous passerine birds. Feathers were collected at locations ranging from Alaska to the southeastern USA. From the isocline map they interpolated to derive estimates of δD values in precipitation at sites where feathers were collected. The correlation between δD of the feathers and that of precipitation at the collection sites was very high ($r = 0.91$). This correlation is the first evidence that there is a tight linkage between δD in feathers and that occurring in the precipitation where the feathers were grown.

To provide further evidence of this relationship, Hobson and Wassenaar[1] analyzed the δD in feathers collected from five species of neotropical migrant songbirds on their wintering grounds in Guatemala. The isotopic ratios of these feathers placed all the individuals within the known breeding range of that species. Based on these and other results Hobson and Wassenaar[1] conclude that 'the large hydrogen isotopic gradient in growing season rainfall across North America currently allows for ready discrimination of distinct breeding populations of songbirds and other organisms on a large scale'. This ability alone makes it likely that this technique will provide new insights into old questions about the biology of migration.

Box 1. Isotopes in avian research

Over the past decade, analyses of stable isotopes of C and N have been applied to a wide variety of problems in avian biology. Laboratory studies of the fractionation of C and N isotopes between bird diets and tissues such as feathers, bone, blood muscle, liver and eggs have established the reliability of these techniques for analyzing avian diets[9]. Analyses of these isotopic ratios can provide important clues about the foraging behavior and environments of animals in the field. For instance, δ^{15}N values have been used to evaluate the relative contributions of marine and terrestrial protein to the diets in gulls[10], northern saw-whet owls (*Aegolius acadicus*)[11], Caspian terns (*Sterna caspia*) and double-crested cormorants (*Phalacrocorax auritus*)[12]. Also, δ^{15}N increases at higher trophic levels and with the age of animals and thus can be used for trophic analyses like those performed on the extinct great auk (*Pinguinus impennis*)[13] and the endangered marbled murrelet (*Branchyramphus marmoratus*)[14].

An additional facet of the analysis of δ^{13}C and δ^{15}N is that turnover rates of these isotopes differ systematically among tissues. In Japanese quail (*Coturnix japonica*), the half-life of C isotopes in tissues varied from a few days for liver to a few weeks for muscle and blood to six months for bone collagen[9]. So, different tissues provide dietary information that is integrated over different time periods. Because the isotope ratios of different tissues represent time-integrated dietary samples, it is possible to reconstruct dietary histories of individuals by comparing among tissue samples.

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Box 2. Molts, feathers and isotopes

The primary molt for most temperate songbirds occurs after breeding and usually precedes autumn migration. This molt is said to be complete because it includes all of the flight and body feathers. Many songbirds also molt in the spring months before breeding, but to a much more variable degree. This spring molt is said to be limited, partial, or incomplete because in most species the flight feathers are not molted.

While feathers are growing they are connected to the blood supply of the bird. As feathers grow, isotopes assimilated through foraging are incorporated into the feather's keratin structure. When feathers are fully formed, the vascular connections to the feathers atrophy and the feathers become inert. For this reason, the ratios of isotopes of elements like carbon are fixed record of the ratios of those elements in the environment where the feathers were grown.

For other elements, like H, the picture is not as clear. Only about 60% of the hydrogen incorporated into feather keratin is carbon bonded[2]. So, if the remaining 40% of hydrogen is exchanged rapidly with environmental hydrogen, then δD values of feathers would have little utility as geographic markers for migrant birds. Fortunately for ornithologists, experiments by Chamberlain *et al.*[2] documented that only 13% of the hydrogen in feathers of American redstarts (*Setophaga ruticilla*) was exchanged with the environment. This finding allowed Chamberlain *et al.*[2] to conclude that post-molt H exchange was unlikely to have a significant effect on their analysis.

The real power of H isotope analysis, however, probably lies in combined comparisons of $\delta^{13}C$, $\delta^{15}N$, and δD in feathers and the surrounding environment. The first glimpse of this power is shown in Chamberlain *et al.*'s study[2]. By combining analyses of the $\delta^{13}C$, δD and strontium ($\delta^{87}Sr$) in feathers, these authors were able to differentiate three regions of the breeding range of the black-throated blue warblers (*Dendroica caerulescens*). Also, the isotopic signatures of feathers collected during winter in Jamaica, Puerto Rico and the Dominican Republic corresponded to locations within the breeding range of black-throated blue warblers. From these findings the authors concluded that isotopic ratios have the potential to serve as population markers for birds and to greatly advance our understanding of migration biology.

Implications for the future

These innovations have particular relevance because of the recent concern over the population status of migrant songbirds[6]. Early concern over the possibility of widespread population declines has given way to a more complex picture of regional and habitat based declines in some species groups and stable or increasing trends among other species groups[7]. Nonetheless, some species and groups of species are suffering long-term sustained population declines that warrant attention. The ability to manage these populations effectively depends on our understanding of the links between breeding, wintering and migratory populations[8]. Toward this end, analyses of stable isotope ratios could play an important role in the conservation of neotropical and other migrant birds.

Beyond these direct applications to conservation, the ability to delineate the migration corridors and wintering grounds of birds that breed in North America is fundamental to our understanding of the ecology of these species. This information will provide new insight into long-standing questions about migration biology, such as the following. Is the timing of passage of individual migrants related to their breeding location? Are particular stopover sites used more frequently by birds that breed in particular latitudinal bands? Do more northerly breeding populations winter in more northerly areas? Do migrants follow the same flyway in both spring and fall? How common is differential migration among sex and age classes? New insights into these basic question have the potential to revise our understanding of bird migration.

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