CHAPTER

10

Outlook for Using Stable Isotopes in Animal Migration Studies

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A quantifiable understanding of animal movement supports a host of research topics, ranging from the evolution of life history strategies to the ecology and physiology of actual migration and dispersal. The lack of basic information on migratory connectivity for most of the world's migratory species remains the most crucial gap in our knowledge, despite this gap is primarily technological and not conceptual (Wikelski et al., 2007). Quantitative knowledge of how individuals and populations are spatially connected between all periods of their annual cycle is the key. Without knowledge of where individuals spend their time during the year, it is impossible to deduce the factors that influence behavioral plasticity, fitness, how populations are regulated, and how environmental changes affect life-history tactics.

As noted in the previous chapters, the past decade has seen tremendous progress in the advancement of the use of naturally occurring stable isotope measurements and associated spatial modeling approaches. However, knowledge gaps remain, and improvements are needed through new research. It is impossible to fully predict how the use of stable isotopes in migration research will progress over the next decade as technological, analytical, and scientific innovations proceed, often in unpredictably novel ways.

In this summary chapter, we put forward suggestions and priorities we believe will be of

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help in closing key knowledge gaps and in further advancing the field.

10.1 SAMPLES AND ISOTOPIC ANALYSES

10.1.1 Isotopic Sampling

Stable isotopic information from migrant animal tissues are useful only if they are unambiguous indicators of the geographic location at which the tissues were grown and can be linked to a relevant isoscape for inferring movement. It is crucial to choose an appropriate fixed or dynamic tissue (bulk tissue or specific compound) that reflects the appropriate period of dietary integration of interest. Critically, we need to know the ecological and physiological factors that determine diet-tissue isotopic discrimination corresponding to that tissue and how that discrimination varies both within and among individuals at a given location or on a given diet. Accordingly, knowledge of the life history and biology of the species of interest is paramount.

New models that link physiological processes of consumers to the processes and patterns of stable isotope ratios in nature will be key to improving the accuracy and precision of geospatial assignments. Improving our knowledge of diet-tissue isotopic discrimination and elemental turnover for organisms of interest will help refine field methods and experimental design. This will likely require controlled captive studies and sampling of wild populations whose diets and nutritional physiology are known, for multiple isotopes, bulk tissues, and specific compounds.

10.1.2 Stable Isotope Analyses

Tremendous progress has been made over the past 10 years for ^{2}H isotope analysis of bulk tissues for determining nonexchangeable H, both on the analytical development side, and by the introduction of new keratinous reference materials to ensure results among laboratories are comparable (Chapter 2: Introduction to Conducting Stable Isotope Measurements for Animal Migration Studies). Hydrogen isotopes, by far, remain the most promising of the light stable isotopes for determining migratory connectivity. Yet, knowledge gaps remain, particularly in our understanding of the H isotope diet-tissue discrimination for most terrestrial and aquatic organisms.

Many of the analytical methods for bulk tissue isotope analyses of CNS are nowadays straightforward and highly cost-effective. Oxygen isotopes (^{18}O), however, remain relatively unexplored and hampered by analytical challenges and poor knowledge of O flow in dietary food webs. We hypothesize that O isotopes will poorly mirror H isotopes, but it remains to be seen whether new and other valuable information is to be gained by tissue ^{18}O analyses (Bowen et al., 2009; Hobson & Koehler, 2015; Wolf, Newsome, Fogel, & Martinez del Rio, 2013).

The analysis of compound-specific C, N, or H isotope analysis of amino acids holds the tantalizing promise of obtaining less ambiguous isotopic connections to dietary isoscapes compared to using bulk tissues. However, the analytical aspects of compound-specific isotope analysis (CSIA) remain difficult, costly, and require the highest levels of isotope analytical expertise and investment. Analytical improvements (ease, lower cost) in CSIA analyses of H and C isotopes of proteins are urgently needed, along with the need for amino acid H and C isotope reference materials to ensure comparable results among laboratories.

Trace element isotopes (i.e., ^{87}Sr) have shown good promise for migratory studies, but barriers remain to routine use, such as the need for specialized laboratories, and the high risk of external contamination without careful precautions and handling. Furthermore, isoscapes for trace element isotopes are only beginning to be developed, and to date have been characterized for few regions.

New laser-based isotope technologies show promise for reducing the cost and improving accessibility of isotope analyses (including field-based analyses), however, the current lack of automated sample preparation devices for bulk tissue C or H isotope analyses hampers any progress in this area, and will hopefully be overcome in the next decade.

10.1.3 Compound Specific Isotope Analyses

The ability to disentangle the signals of baseline isotope variability from trophic dynamics with compound-specific stable isotope analysis of individual amino acids (CSIA-AA) has opened new doors to studying animal migration, habitat use, and foraging ecology. To realize the full potential of CSIA-AA in ecological studies, we need several major improvements on both the analytical and theoretical fronts.

There is an obvious need for controlled laboratory and field studies examining the patterns, magnitudes, and variability of isotopic discrimination of individual amino acids, as well as the rates at which those isotopic signals turnover in consumers. With this comes a need to improve the CSIA-AA community's collective understanding of the underlying physiology and biochemistry driving patterns in isotopic discrimination at the compound-specific level (O'Connell, 2017).

As more and more studies use CSIA-AA approaches, the need for standardization of procedures and corrections, reference materials, and chromatography interpretations to enhance QA/QC becomes even more important (e.g., Ohkouchi et al., 2017). This will require more communication across laboratories, with exchange of reference materials and protocols to improve QA/QC and make the data and associated interpretations comparable across studies. We also need continued method development to make these CSIA techniques faster, cheaper, and more efficient if we ever hope to see these powerful tools become more than a fringe endeavor pursued by a limited number of labs. As the analytical, methodological, and theoretical commitment to understanding CSIA-AA grows in the ecological community, so will the power of these approaches to studying movement and foraging ecology.

10.2 MIGRATORY SYSTEMS

10.2.1 Avian and Insect Migratory Systems

Stable isotope applications in tracking bird movement are clearly an area where the most progress has been made over the past 20 years. Nonetheless, there continues to be a host of areas of concern and needed developments (Hobson, 2011; Martinez del Rio, Wolf, Carleton, & Gannes, 2009). Fortunately, birds molt at predictable periods of the annual cycle and these patterns are generally known for most species. So, feather isotope values can usually be associated with breeding, wintering, or molt migration regions. However, the variation we see in δ^2H values within single wild populations (i.e., growing tissues at the same general location) is poorly understood. Understanding contributions of isotopic variance within populations related to diet, age, individual physiology, and microhabitats will be important. On the other hand, the establishment of reasonable estimates of overall isotopic variance in feathers and other tissues and how this variance might be attributed to predictable factors like habitat and feeding and migratory guild will be of tremendous use in moving toward better assignments of individuals and populations. Associated with this are refinements to tissue-to-precipitation isoscape discrimination based on calibration algorithms used in all assignment approaches.

Application of isotopic methods for tracking small migratory insects are still in its infancy (Hobson et al., 2018) even though the size of most insects makes them ideal candidates for this technique. Unlike birds and other animals, insects are amenable to controlled experiments whereby isotopic variance and calibrations between chitinaceous tissues and water sources can be established. Thus we expect to see rapid advances in the use of isotopes for migration insect research in the next 5–10 years. Future experiments should investigate how isotopic patterns can be affected by life-history strategies such as within-soil versus above-soil larval stages. Many migratory insects of interest are associated with crops (i.e., pests) and the use of irrigation waters may be a confounding factor in establishing appropriate water-based isoscapes.

10.2.2 Marine Migratory Systems

The use of isotopic tracking methods in marine and aquatic systems has been limited by a lack of reference isoscapes. With increased interest and effort invested in developing both sample-driven and mechanistically modeled CNS isoscapes, we anticipate wider use of isotopic methods in marine migration ecology, particularly in fishes. Methodological advances lowering sample mass required for C and N isotopic analyses open the potential for incremental sampling of the macromolecular framework of otoliths. This would allow retrospective analysis of lifetime fish movements drawing on the millions of otoliths routinely sampled (and often archived) as part of fisheries surveys. Studies on freshwater fish migration are also limited.

More effort is needed to quantify and predict the extent and scale of temporal variability in baseline aquatic isoscapes and the implications of temporal variability for isotope assignment methods. Mechanistic modeling is likely to be critical to cover the scale of marine isoscapes, but field data are crucial to testing the validity of model simplifications and assumptions. We repeat the longstanding call for more experimental and modeling studies quantifying and explaining physiological fractionation of C and N isotopes within taxonomically and functionally varied marine and aquatic organisms and their tissues.

10.2.3 Mammal Migratory Systems

Isotopic tracking of terrestrial mammals has been conducted successfully over the past decades, yet the application of stable isotopes for tracking mammals is impaired by low spatial mobility of most terrestrial mammals, at least compared to migratory birds or insects. Owing to their lower mobility, migratory mammals do not cross necessarily wider areas of distinctive isotopic patterns, which is a key prerequisite in isotopic tracking. The spatial resolution of the isotopic tracking approach could be greatly improved if more reference data on the isotopic composition of nonmigratory mammals were available. This would help in establishing isoscapes that are specific for certain mammal taxa or feeding guilds. Further, captive studies may inform us about the causes of variation in stable hydrogen isotopic composition in keratinous and nonkeratinous material. This will eventually lead to improved isotopic transfer functions that support more fine-scaled tracking of mammal movements. Approaches that combine isotopic tracking with complementary tracking methods such as GPS or geolocators might help in evaluating the accuracy and precision of the isotopic methods in mammals. First and foremost, we need more hypothesis-driven experimental studies conducted under controlled conditions to learn more about the kinetics of stable isotopes, in particular those of hydrogen and oxygen in mammal body tissues. To this end, we need more isotopic studies that address physiological questions in an ecological context and vice versa. This will inform us about promising research directions in the spatial tracking of mammals based on stable isotopes.

10.3 ISOSCAPES AND ASSIGNMENT

The success of using isoscapes in migratory studies rests on several interdisciplinary pillars which will require more attention in the coming years. The development and application of theory, geospatial data, and quantitative tools to predictively describe isotopic variation in the environment has been a focus of research for over a decade, but significant opportunities remain for improvement. Recent work has continued to advance our capabilities with respect to modeling environmental waters, and significant developments for others isotope systems such as carbon and strontium have been made. However, the isoscape research community is just beginning to scratch the surface in terms of the information resources available to support such work. Large amounts of isotopic data remain unpublished, unavailable in reports and institutions, or in papers, and with the right tools and could be gathered from the literature and used to support isoscape modeling. The capture and use of new data to support these efforts needs to become efficient (Pauli et al., 2017). Modeling tools from the atmospheric and Earth science communities could be leveraged to support improved predictions (Gibson et al., 2010; Risi et al., 2012), remote-sensing data continue to grow in scope and coverage and could inform many isoscapes, and data resource projects such as seamless geological maps are in process that promise additional potential for advances.

A predictive understanding of the isotope discrimination processes that occur between ingestion of the animal's water or food and the production of the animal tissues should be developed and incorporated into the isotopic assignment process. As emphasized earlier, this cross-cutting need will require integration of behavioral and physiological theory with data and experiments. Because this understanding would address potential sources of both bias and uncertainty it will be integral to advancing all isotopic assignment work, whether based on environmental isoscapes or more directly on known-origin data. In an ideal world, isoscape-based assignments conducted 10 years hence might allow consideration of an individual's age, sex, and physiological status, as well as other accessible properties such as weather, phenology, and environmental heterogeneity at potential places/times of origin, to provide the most accurate and robust assessment of origin possible.

Significant scope remains for the isoscape community and quantitative ecologists involved in methods development of tools for isoscape-based assignment to broaden the accessibility of these methods. The statistical methods available for building isoscapes and performing the assignment of migratory animals lie at the forefront of modern applied statistics. Users can choose advanced frequentist methods based on mixed models or advanced Bayesian methods based on MCMC sampling, which both consider and propagate many sources of uncertainty previously neglected. Challenges include the distribution of existing and upcoming methods, and the distribution of reference datasets. Publications, no matter how detailed, are insufficient to allow one to implement methods developed by others. Generalizing the exchange of computer scripts, using R, e.g., would help solve this limitation. It would allow users to implement different methods with minimal difficulties and would offer the opportunity for developers to study the different methods in detail. The practice of publishing code exists in the field (e.g., Vander Zanden et al., 2014; Chapter 9: Isoscape Computation and Inference of Spatial Origins With Mixed Models Using the R package IsoriX) but is not widespread.

Sharing isoscape reference datasets is also crucial. Combining efforts to share data of reference calibration samples for different taxa would lead to more accurate assignments than sharing the calibration estimates alone. Relying on common calibrations would also help to control an important source of variation among assignment studies. Sharing reference data would further allow users to learn how to use a given method from the replication of known results and developers to compare different methods under the same conditions. For the sharing of computer code and data to be efficient, it is necessary that they come with nonrestrictive copyright. Since publication of the first edition of this book several platforms supporting such analyses have been released, including the web-based IsoMAP toolkit (http://isomap.org) and the IsoriX R package (https://cran.r-project.org/web/packages/IsoriX/index.html). Other researchers remain involved in development of purpose-specific but potentially generalizable software tools for such analyses, and it is both clear and exciting that the research community is beginning to engage in a process of documenting and disseminating these research tools.

10.4 LINKING STABLE ISOTOPES TO OTHER SPATIAL MARKERS

There is no doubt that the revolution in the miniaturization of electronic devices for tracking migrant animals will continue to have a tremendous influence in studies of animal movements. However, as we have stressed throughout this book, stable isotopes offer a powerful complimentary tool with distinctive advantages. The most important of these is the absence of bias to site of marking of individuals, low cost, no interference with animal behavior, and the extremely small sample sizes required for analysis. Every capture is a recapture.

However, there are numerous intrinsic and extrinsic markers that add a degree of geographic information to stable isotope approaches and all recognize that the clever blending of numerous tools will be the only path forward. These include, but are not restricted to, measurements related to the use of Bayesian priors in assignment models such as genetic structure, fatty acid composition, contaminant load, morphometrics, ring recovery vectors, and density distributions (Royle & Rubenstein, 2004; Rundel, Wunder, Alvarado, Ruegg, & Harrigan, 2013; Rushing, Ryder, Saracco, & Marra, 2014; Van Wilgenburg et al., 2011). It follows that the certainty of assignment of a migrant's origin may (but not always!) be improved by linking isotopic patterns with geographic information from other sets of nonisotopic data.

While the ability of other markers to provide geographic information is well established, there has been little work on defining the limits of resolution for each marker or assessing the possible benefits and accuracy of combining multiple (isotopic and nonisotopic) markers or related information. Evaluating the limitations of combinations of isotopic intrinsic markers will be important for understanding which types of questions are best addressed with which combinations of markers.

10.5 RESEARCH IN SUPPORT OF CONSERVATION

Finally, while we have not emphasized important conservation efforts to protect threatened migratory phenomena, in the next decades we may witness catastrophic declines of many migratory taxa (Wilcove & Wikelski, 2008). We share a responsibility to conduct meaningful research quickly and effectively to define migratory connections, and to use this information and data to inform conservation actions (Faaborg, Holmes, Anders, Bildstein, & Dugger, 2010; Knight et al., 2008). It is insufficient to endlessly refine and debate the merits of calibration algorithms and isotopic variance, or the pros and cons of this model versus that model. While these pursuits are important and help to refine our approaches, conservation action depends on focusing on answering larger scale questions such as are northern populations declining faster than southern populations and can these trends be related to factors operating on the breeding or wintering grounds or both? Stable isotopes will continue to be a powerful advisory tool for conservation, and it is our duty to ensure that meaningful and actionable results are conveyed to conservation managers.

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