CHAPTER 6

Future Directions and Challenges for Using Stable Isotopes in Advancing Terrestrial Animal Migration Research

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I. INTRODUCTION

It is clear that a detailed understanding of animal movements underpins a host of fundamental research topics, ranging from the evolution of life histories, behavioral plasticity, and constraints to the genetic basis for migration and dispersal (Chapter 1). However, it has been pointed out on numerous occasions that our great lack of information on dispersal and migration represents one of the most formidable

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gaps in our knowledge. This gap sits at the core of our understanding of animal ecology and evolutionary biology (*e.g.*, Koenig *et al.* 1996). Surprisingly, the obstacle for closing this information gap is primarily a technological one rather than a conceptual one (Wikelski *et al.* 2007). Breakthroughs derived from technological advances will no doubt also shed new insight into theoretical and conceptual models at both the individual, and population level. Simply put, technological advances in animal tracking has and will continue to vastly improve our understanding of nearly every aspect of organismal, population, and community ecology.

The advent of stable isotope methods as well as other intrinsic markers has coincided with important developments in the technology of animal tracking using extrinsic markers. Thus, we find ourselves at a point in time where new and diverse developments are occurring on a number of research fronts. In this chapter, we examine the path ahead and, in particular, how stable isotope approaches can be best combined with other promising and new techniques.

II. THEORETICAL CONTEXT

While we have argued in this volume for the general case that stable isotope approaches will continue to bear fruit in studying animal migration, we believe that even more progress can be made by research that is very specific in its objectives. That is, we should focus on key questions that have the highest priority for advancing our knowledge of dispersal and migration ecology. Keeping a clear focus on key questions will help avoid the pitfalls of following methodological and shotgun approaches that may provide little insight into questions of biological significance.

Recently, deliberations from a network of migration biologists have proposed four key research questions (see Migrate website at http://www.migrate.ou.edu) that we also think require immediate attention. These four research questions are given below:

1. What are the determinants of behavioral plasticity in migrant animals and what are the constraints on behavioral adaptation? For example, how do individual migrants cope with, say, weather-induced uncertainty over the short-term, and under what circumstances are populations not able to adapt to long-term environmental changes?
2. What are the determinants of individual fitness of migrants? In particular, knowing when and where most mortality occurs and the environmental and biotic events that contribute most to variation in mortality rates would be very useful.
3. What are the drivers of population dynamics in migratory animals? Having good estimates of vital rates that could be used for population projections and understanding which vital rates are most sensitive (or elastic) would be a major advance.
4. What is the impact of environmental change on migratory life histories? In particular, what are the impacts of land use, environmental, and climatic changes? Ultimately, critical evaluation of predictions regarding changes in population dynamics and individual behavior and adaptation in response to land use and the environment will be the measure of advance in our science.

The spatial and temporal extent of research studies designed to examine the role of behavioral plasticity will likely differ from those that examine long-term impacts of environmental change. Nonetheless, it is useful to have these questions clearly in mind during discussions of how to improve (1) the kinds of isotope data we collect and (2) the geospatial information that we can extract from those data. All of the above questions require knowledge of how individuals and populations are spatially connected between all periods of their annual cycle. Without knowledge of where individuals are spending different periods of the year, it is impossible to infer the factors that influence behavioral plasticity, what are the primary factors that influence fitness, how populations are limited and regulated, and how environmental change can affect life-history tactics. In this context, we examine some outstanding challenges and limitations that are needed to address these evolutionary, ecological, and conservation questions in the future. We place special emphasis on those areas where innovation is needed to overcome known obstacles.

III. CHALLENGES AND LIMITATIONS

The following discussion is divided into two interrelated questions that portray the challenges and limitations of trying to predict the origins of animals from stable isotope values obtained from their tissues. First, how can we improve the collection and analysis of stable isotope data to infer origins of a particular migrant or population of migrants? Second, how can we extract more information from the isotope data we collect so that we optimize our ability to assign migrants to sites of origin? These two issues are at the heart of understanding the ways in which we can increase the utility of isotopes as spatial markers and what obstacles might lay in the way.

We know that significant sources of variation exist when using stable isotopes to track migratory individuals. Asking what would be an "ideal situation" can provide some guidance as to what components of variation we should be addressing. An ideal situation for tracking migratory animals would be one where we were able to sample all of the potential sites of migrant origin, all isotopic data had very high degree of spatial structure, no within-site variation, and every individual had the same diet and physiology (and thus the same diet-tissue discrimination factor). Ideally, the tissue sampled 100% reliably grown at a known location and would be biologically inert once grown. The ideal situation would also have no seasonal variation in the isotopic values of the energy and hydrological cycles that fuel primary producers and drive the food web. And, instrumental error would be zero.

Obviously, fully ideal situations do not exist but we can deal with these factors causing variation in two ways. We need (1) a better understanding of the mechanisms that drive the observed isotopic variation so we can adjust the design of future studies and (2) to incorporate this variation into our statistical methods for assigning individuals to places of origin. We address both of these topics below.

A. Toward Better Isotope Data

What are "better" isotope data? To us, this means isotope data from a migrant animal's tissues that provides the most unambiguous indicator of the geographic location at which the tissues were grown. As discussed in Chapter 3, it will be crucial to choose the appropriate tissue that reflects the appropriate period of dietary integration of interest. We also need to know what ecological and physiological factors determine the diet-tissue isotopic discrimination factor corresponding to that tissue and how that discrimination varies both within and among individuals at a given location or on a given diet. While several studies have provided useful working estimates for a number of tissues representing a number of species, especially for δ^{15}N and δ^{13}C, we now know that diet quality and physiological state of an animal can influence such factors. It is also clear that we have very little idea of how migration per se can affect the behavior of isotopic signals in animals because few studies have been able to mimic migration as part of the experimental protocol (Hobson and Yohannes 2007). This is true also for estimates of isotopic turnover rates in tissues of exercising animals appropriate to applications involving individuals in the wild. The situation becomes even more complex when we consider the use of hydrogen isotope measurements in tissues because of the additional opportunity for hydrogen isotope exchange within animals and for the distinct roles of diet and drinking water that will influence tissue isotope measurements.

There has been a long-standing call for improved and experimentally based foundations for stable isotope approaches (*e.g.*, Gannes *et al.* 1997). We must consider more directly what is required to improve isotopic studies of migration. Captive rearing experiments are needed that will pay far more attention to the composition of diets with a view to replicating as closely as possible the nutritional range experienced by migrating animals of interest (*e.g.*, Pearson *et al.* 2003). Researchers using δ^{15}N and δ^{13}C must consider and report the elemental C:N ratios for the foods they use because this will give an indication of the protein content and assist with estimates of the appropriate nitrogen isotope discrimination factor to use. Recent research has also demonstrated the value of considering metabolic pathways associated with the macromolecules of proteins, lipids, and carbohydrates over bulk tissues. Here, it may be most useful to consider all possible sources of an element in the tissue of interest. We also require more information on how prolonged exercise associated with migration affects isotopic discrimination and elemental turnover rates, studies best accomplished using wind tunnel experiments for example. Similarly, effects of age and sex, especially related to physiological condition or reproduction, would be useful areas of research using stable isotopes.

These developments underscore the need to better combine disciplinary expertise in animal physiology and biochemistry together with that of ecology and stable isotopes. The more closely we can mimic physiological conditions related to migration, reproduction, molt, and migratory preparation in captive animals along with predictive isotopic models, the better we will be able to model behavior of stable isotopes in wild migratory animals. This rigor is especially needed for δD and δ^{18}O for which little is known about physiological and dietary factors determining the isotopic composition of animal tissues. In the short term, emphasis should be placed on fixed keratinous tissues and blood components because these two are proving to be of the greatest use in migration tracking. However, understanding factors that determine δD and δ^{18}O values of muscle, lipid, liver, and bone collagen will be of importance. So, we can look forward to the development of a series of models that carefully link tissue-specific δD and δ^{18}O values of organisms with predicted or measured surface water, ground water, or mean precipitation values. There are many emerging examples in which physiology, apart from habitat choice and diet, is crucial to understanding the isotope ratios of an individual's tissues (Chapter 3). Models that couple physiological processes of consumers with the physical processes that drive patterns in stable isotope ratios in the environment will be a key for improving the precision of geospatial assignments. These physiologically informed models can be directly incorporated into probability density functions that can be used to map the origin of migrants. Thus, we can imagine models that take the available geospatial isoscape data and combine it with information on body size, tissue type, level of exercise, species group, and perhaps migratory diet to assist us in making the most of our isotope data.

Once we have increased our knowledge about the fundamental currencies of diet-tissue isotopic discrimination and elemental turnover for organisms of interest, we can consider other aspects that include refining our field methods and experimental designs. So far, good progress has been made on providing estimates of these parameters for birds, but far more work is required to explore sources of variation. Very little data exist for other animals such as insects and mammals.

B. Problems of Confidence and Precision in Geospatial Assignment

As developed by Wunder and Norris (Chapter 5), the ideal situation to infer origins of migratory animals from isotopic analyses of their tissues will be to have as complete a picture of the isoscape from which that animal's tissues were derived. This picture includes a good appreciation of the degree and causes of isotopic variation at single locations. As a minimum, studies should attempt to estimate the isotopic variance among individuals from known locations for each tissue of interest, within tissue variance for the species of interest, laboratory measurement error, and an estimate of the error associated with the isoscape model being used. The use of nonisotope information about the relative probability of origin is also encouraged. A Bayesian framework provides a way to formally quantify multiple sources of information about the relative probabilities of origin, but insights can also be gained from stepwise analysis that iteratively partitions the geospatial extent of potential origins.

Ongoing developments in GIS applications and remote sensing information layers will be extremely useful for narrowing possible sites of origin. An obvious example would be a species that only occupied forested habitat or those only occurring above a certain elevation. As habitat requirements become better understood for various taxa, those habitat types can be mapped using spatially explicit datasets. Narrowing possible areas of origin from more detailed information will help researchers to (1) develop sampling strategies for developing robust species-specific isoscapes and (2) reduce the potential amount of regional variation of isotopes in environmental samples.

Researchers should also consider optimal sample sizes of individuals that will provide the best estimate of different components of variance. In this sense, the isotope approach is no different from any other type of ecological sampling. Unlike most other ecological sampling, however, all such estimates are confounded by measurement error. That is, the δ-values are not known exactly, so estimates of population standard deviations based on the observed δ-values are always "underestimates." Other than Wunder (2007) and Wunder and Norris (2008), the impact of measurement error has not yet been fully explored. Field studies that document the isotopic variance in populations of organisms from single locations and that attempt to tease out the environmental or physiological causes of that variation are very much needed. In addition to captive studies, meta-analyses of datasets across species and isoscapes may prove to be useful in identifying and better understanding between-individual variation in tissue isotope values.

There are also the challenges of integrating spatial demographic data with isoscapes to arrive at a continuous picture of migratory connectivity. However, we are often more interested in migratory dispersal and connectivity *among* populations. That is, the rates at which demographic units exchange individuals (Salomonson 1955, Webster *et al.* 2002, Chapter 5). These rates can often be estimated with more certainty than can the geographic coordinates from which an individual originated. However, most previous studies of migratory connectivity have used arbitrarily defined regions or populations to develop assignment likelihoods (*e.g.*, Kelly *et al.* 2005). Few studies have attempted to add demographic parameters to their models. As we begin to try to merge information on precipitation isotope ratios, tissue isotope ratios, and organismal demographic data, concerns about matching the proper temporal scales are exacerbated. The more information available on the demographic structure of populations, the more we will be able to define appropriate population boundaries for use in assignment using stable isotope approaches. Such demographic data might be provided with the careful use of genetics (see below).

As modeling frameworks become more technologically sophisticated, the challenge of making them and the results accessible to a wide range of research and wildlife management audiences becomes important. Many of the user and client groups who would most benefit from applications of advanced modeling approaches have difficulty accessing (or even understanding) these new approaches. In order to expedite both the development and distribution of novel models, it will be important for modelers to work alongside ecologists, physiologists, and biochemists to push the frontiers of the field, and to clearly communicate the findings to environmental groups and managers.

C. Stable Isotope Measurements

There are a number of needs for improving the analytical methods used in stable isotope studies. Most of these relate to hydrogen isotope exchange issues in keratins and other organic tissues (Chapter 2). One pressing issue is the need for organic tissue laboratory standards where the hydrogen isotope ratios have been validated in multiple laboratories that apply similar sample preparation methods. Another problem is the lack of organic H standards spanning the positive and negative ends of range of values, encountered in migrant animals. The absence of widely available standards spanning the entire isotopic range contributes bias in the correction for exchangeable and nonechangeable hydrogen at both ends of the observed range. A third issue is the lipids within and external to the sampled tissues. It is clear that decisions on what solvents are used to clean tissues can have significant effects on the measured isotope values (Post *et al.* 2007). However, there is no consensus on the best methods for treatment of particular tissues prior to isotope analyses.

It is possible that other advances could be made through compound-specific isotope analysis (CSIA) of amino acids, fatty acids, or other compounds within specific tissues. Analysis of the isotope ratios of specific compounds have the potential advantage of providing a more direct linkage between the environment (*i.e.*, via diet) and the migrant's tissues. If the appropriate compound were chosen, the potential to improve the geographic signal from the environment may be considerable. For example, essential amino acids do not appear to undergo isotopic discrimination between diet and a consumer's tissue. Thus, in cases where the diet or trophic level of the organisms is unknown, the use of these essential amino acids could reduce variance in baseline food web signatures, especially for $\delta^{13}C$ and $\delta^{15}N$ measurements. Compound-specific analyses using deuterium measurements of animal tissues are in its infancy and it would be extremely useful if there were similar compounds involving hydrogen and oxygen that could provide information on baseline water isotope values without the complications of physiological reprocessing, isotope discrimination, and isotope exchange within the animal. To date, there have been relatively few compound-specific isotope studies with demonstrable links to migration research. However, Popp *et al.* (2007) recently demonstrated the utility of distinguishing between "trophic" amino acids (*i.e.*, those showing enrichment with trophic level such as alanine, aspartic acid, and glutamic acid) and "source" amino acids (glycine and phenylalanine) in delineating aspects of the ecology of migratory tuna (*Thunnus albacares*). Gleixner and Mugler (2007) recently demonstrated the potential in using compound-specific hydrogen isotope analysis of *n*-alkanes to infer past climate from lake sediments. The use of compound-specific hydrogen isotope analyses in migratory wildlife would represent a completely new area of research that may be able to explain some of the variance observed among individuals. Other areas of interest for researchers of animal movements will be the use of compound-specific measurements to identify point-source compounds or pollutants of anthropogenic origin (Evershed *et al.* 2007). As noted in Chapter 1, the use of spatial patterns in the occurrence or concentrations of contaminants and other compounds in the environment can provide information on origins of migratory animals. The addition of CSIA may well improve the resolution of such approaches, and researchers should always be cognizant of the delineation of spatial patterns in any environmental compound, should there be an appropriate application to tracking migrant animals.

There are caveats that go along with this call for new compound-specific assays. The isolation and analysis of specific compounds are comparatively difficult, and therefore far more expensive than bulk tissue isotope analyses. Also, CSIA are exceedingly time consuming and thus it may never be possible to achieve the rapid throughput or to facilitate the numbers of samples that allow us to generate the large sample sets needed for statistical analyses of large-scale sampling efforts. If the dietary sources of the specific compound, for example an essential amino acid, are not more homogeneous in their isotopic composition than the bulk diet, then no increased resolution would be expected. Finally, in the case of hydrogen, if the portion of the specific compound of interest (*e.g.*, the H atoms of an essential amino acid) is exchangeable with those in the environment, then there will be substantial variance introduced into the process. These caveats have been largely responsible for the slow development of CSIA despite several successful applications to ecological questions (Evershed *et al.* 2007).

D. Improving Isoscape Models

The utility of isoscapes rests on our understanding of the fractionating processes that occur between ingestion of the animal's water or food source and the production of the animal tissue or compound being measured, and the accuracy with which we can map the spatial variability of that source. Therefore, improvements in models describing and mapping this spatial variability, as well as models describing fractionations associated with animal metabolism will significantly improve the utility of isoscapes to address questions in animal ecology and evolution. While it would be ideal if all potential areas of origin differed categorically in their stable isotope values, this will almost never be the case across an entire range of a species, especially when attempting to differentiate between climatically or geologically similar regions. Despite this real-world limitation, there is significant potential for improvement in assignment of migratory individuals and populations using isotopes through increases in the accuracy of isoscape models and improved statistical assignment techniques (Chapter 4 and 5).

What are some ways that existing models can be improved to extract more information from the available data? One possibility is through downscaling of isoscape models to a resolution of kilometers, meters, and perhaps finer scales, although as noted in Chapters 4 and 5, this approach must be carefully balanced by concurrent increases in the resolution of the data and spatial specificity of isoscape models. There are multiple challenges here that relate to problems of small-scale heterogeneity and medium-scale homogeneity in isoscapes (Chapter 4 and 5). The stable isotope ratios of both N and C can vary over just a few meters, while H and O isotopes scale over large areas, even within biogeographic regions that share similar δD and δ^{18}O values. These scaling issues have an important impact on the certainty by which we can assign origins. Combining multiple isotope ratio measurements (*e.g.*, C, N, H, and O) may in some cases improve model predictions, especially when elements whose isotopic variations are discrete (*e.g.*, Sr) are combined with those with more continuous variation (*e.g.*, H, see Chapter 4). Work in the future should address these limitations directly, potentially improving the information that isoscapes and tissue- or compound-specific isotope ratio analysis yield.

An additional avenue that is just beginning to be explored is the improved characterization of isotopic variation in food webs over temporal scales. Thus, an additional unanswered question is how can the observed isotopic variation among and within years be used to improve predictions for migratory species over specific time frames? These temporal challenges will initially require specific assumptions about the mechanisms and time lags that influence isotope ratios of animal tissues, but should also spur important mechanistic research to improve our understanding of these dynamics. As this work progresses, there is significant potential for the development and application of improved isoscape models that capitalize on temporally resolved satellite and climate data to predict spatial isotopic patterns for discrete temporal intervals of relevance to specific migration research problems.

E. Linking Stable Isotopes and Other Geographic Markers

There are numerous intrinsic and extrinsic markers that can add some level of geographic information to stable isotope approaches. 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 intrinsic or extrinsic markers. While the ability of other markers to provide geographic information is well established, there has been little rigorous work on defining the limits of resolution for each marker or assessing the possible benefits and accuracy of combining multiple (isotopic and non-isotopic) markers. Evaluating the limitations of each combination of intrinsic markers will be important for understanding which types of questions are best addressed with which combinations of markers.

The potential to combine innovations in intrinsic and extrinsic markers to track individuals and populations opens a wide array of exciting research questions that to date have been impossible to address. First, extrinsic markers could be combined with isotopes to improve the ability to assign individuals of unknown origin. One of the most obvious avenues that has not yet been explored in a rigorous manner is integrating information obtained from stable isotopes with band recovery data. For example, a few individuals of a species may be marked on the breeding grounds and recovered on the wintering grounds. This information could be used as a prior probability of origin before assigning wintering individuals to breeding areas using isotopes. In this case, information on band recoveries need not be confined to the wintering period. Recoveries during migration can provide useful prior information about the general direction of migration and, therefore, help resolve assignments where isotopes do not have spatial resolution to do so.

The potential to combine innovations in intrinsic and extrinsic markers to track individuals and populations opens a wide array of research questions that, to date, have been impossible to address. The rarity of such studies reflects the degree to which technological hurdles prevent most researchers from employing this strategy. Certainly, any study employing satellite or other tags that produce precise journeys or origins of individuals should, if the individual is recovered, sample those tissues for which the provenance of the period of integration is known. This would provide a means of determining how well our isoscape models relate to reality, a type of "field validation" or "ground truth" that has been impossible to obtain so far.

Genetic markers are inherited and fixed for the life of an individual, whereas isotopic markers are generated continuously. Thus, these two markers provide different (and potentially complementary) kinds of information. Genetic markers can provide information about the natal population for a migratory animal whereas isotopic markers provide only information about the recent origin of an individual from the previous season. This means that these two types of information could provide different estimates of origin. In such cases, the individuals that do not seem to "fit" could be very informative. For example, if the genetic data suggest membership in population A, but the isotope data suggest membership in population B, one possible explanation is that the individual was born into population A, but dispersed into population B. On the other hand, using genetics to estimate recent patterns of connectivity between seasons may be slightly misleading. Applying genetic markers for this purpose should ideally incorporate the probability that an individual greater than 2 years of age dispersed away from its natal site to a new breeding area. The other obvious limitation in using genetic markers is that individuals of unknown origin can only be assigned to the breeding period which means they are less useful when used to assign individuals to other periods of the annual cycle.

Present obstacles to better integration of isotopic and genetic data derive from three main sources. First, the number of genetic markers for which it is possible to examine geographic patterns is enormous. Much of the existing research has relied on mitochondrial DNA phylogeography. It seems likely that patterns detected with these markers could be improved through use of amplified fragment length polymorphism (Irwin *et al.* 2005) and single nucleotide polymorphism methods (Bensch *et al.* 2002). However, methodologies and the number of possible genetic markers continue to expand exponentially making it difficult to develop an efficient method of integrating genetic results with stable isotope ratios. A second problem is that most genetic markers can be measured more efficiently when the DNA samples are isolated from blood that creates some tissue mismatches for isotope analyses based on keratins. This tissue mismatch can potentially be useful in measuring dispersal. Finally, genetic data, by definition, is not continuous but rather categorical which requires different approaches for geospatial representation (Guillot *et al.* 2005, Manni *et al.* 2004). For this reason, the integration of genetic and isotope data in geospatial analyses has lagged development in these separate fields. Progress will require collaboration between isotopists and geneticists with expertise in geospatial modeling (a rare combination!). Any progress arising from this collaboration would have an immediate impact.

In particular, we appear to be at the beginning of a proliferation in the use of stable isotope methods to answer questions about dispersal ecology. The basic idea is that dispersing animals would appear as outliers (genetically, isotopically, or both), after considering the full range of variation estimated for a given location. One difficulty with this approach is that individuals sometimes grow feathers at alternate points in the life cycle. For example, we might assume a feather is grown during the late breeding season on the breeding grounds, when it was actually grown during migration. To separate these cases from true dispersal, having a unique population genetic marker would be useful. Immediate dispersers would have both rare isotope ratios and rare genetic haplotypes compared with the rest of the breeding population. In a similar way, if the isotope data suggest membership in a breeding population (A), but the genetic data suggest membership in a different population (B), this combination of results might suggest that dispersal from population B into population A occurred in a previous year. Demographic information on return rates or apparent survival is another type of information that can be readily incorporated with isotopic and genetic data to estimate breeding dispersal. For example, if we find that 60% of marked adults return to their breeding site between years, we can use this estimate as a prior probability before assigning individuals using intrinsic markers. Similarly, we may have prior information from marked individuals on dispersal distances that can be easily incorporated into probabilistic assignment tests.

Several previous papers have alluded to the use of trace element and heavy isotope analyses to infer origins of migratory animals. To date, trace element profiles, where a suite of elements are measured for relative abundance, have shown significant variation among subpopulations and so appear to have both potential and complications. This is especially the case for species that are known to congregate in a few breeding or wintering sites. Problems arise for cases where species are more diffusely spread across their ranges. Here we face the problem of having little *a priori* information on existing or expected elemental profiles corresponding to origins. Clearly, a much closer collaboration between researchers of animal migration and geologists or earth scientists familiar with regional or continental patterns of trace elements is required. Rather than considering a suite of elements in a multivariate sense, it is likely to be more productive on a case-by-case basis to consider the potential of geographical origins using a few key elements. We can imagine scenarios where deuterium analyses provide reasonable constraints on latitude of a migratory population and some trace elements (like copper or zinc) then provide additional information on origins within that range. The usual caveats of ground-truthing of elemental signatures of organisms from known locations still apply.

Our emphasis in this volume has been on the use of the light stable isotopes (C,N,H,O,S). A few studies have also used Sr isotope measurements because these vary geographically according to the age of the substrate and also differ between marine and terrestrial origins. The stable isotopes of Pb also show considerable potential to provide information on location because this element too is known to vary isotopically regionally. Whereas analyses of the heavier stable isotopes have been the domain of a few highly specialized laboratories, new technological developments (*e.g.*, inductively coupled plasma mass spectrometry) have now opened up the more common use of these and a number of other isotopic measurements. Again, it will be critical to increase our knowledge of the variance associated with isotopic ratios of the heavier elements in any given region of interest. In the short term, it would be most useful to test the utility of combining heavy and light isotope measurements to those species or populations that are reasonably tightly constrained geographically and that show the potential of occupying different geological substrates.

IV. SUMMARY

The intent of this volume was to provide the reader with a comprehensive background needed to understand the potential and the state-of-the-art in the application of stable isotope tools to the study of animal migration, and to encourage new research endeavors. Animal migration remains an exciting field that will provide many years of research for scientists in numerous disciplines. We have hopefully conveyed the idea that stable isotopes are not a "silver bullet" that will provide unambiguous insight into animal origins. The true potential of the isotope techniques will only be realized in cases where the researcher has been careful to first choose the species and migratory system that shows promise isotopically, and then considers the sources of variance in the model used to infer origins. The path ahead will involve far more emphasis on understanding the mechanisms that can influence isotopic variation spatially and within organisms of interest. It will also involve more careful consideration of how we statistically infer origins or establish the probability of assignment. Use of more refined isoscape models that involve several elements and the careful use of new remote sensing GIS layers will also be a fruitful area of research. Obviously, these areas of research and development are likely well beyond the scope of any single researcher or laboratory, and hence this field is sure to emerge as one of the best examples of multidisciplinary collaborative research.

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