

Chapter 13

Using Isoscapes to Track Animal Migration

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13.1 Introduction

Animal migration is a phenomenon that has captured the imagination of scientist and layperson alike and continues to fascinate as new insights into the biological mechanisms behind these movements are uncovered. No less fascinating have been the myriad of innovative tools researchers have used to monitor animal movements and to establish linkages between individuals and populations as they move throughout their annual cycles. These tools can broadly be categorized as exogenous and endogenous (reviewed by Hobson and Norris 2008). Exogenous markers are those devices affixed to an animal for later retrieval and so facilitating a mark-recapture approach or as active transmitters that broadcast the location of an animal via radio- or satellite-based technology. More recently, geographic locator tags have been developed that monitor time and daylight cycles that can ultimately be translated into latitude and longitude once downloaded at recapture. However, the most widely used and versatile exogenous marker has been a simple numbered tag or leg band and to date, millions of migratory birds have been so marked. This approach has been moderately successful for those individuals with a high probability of recapture such as hunted species, those with high site fidelity, or those that congregate in large numbers (Hobson 2003). However, the technique is clearly inadequate for most of the world's migratory organisms. This has led to a great deal of interest

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in the utility of naturally occurring endogenous markers such as stable isotopes and genetic markers. The primary advantage of such approaches is that they do not require initial marking of the organism and so are not biased by the nature of the often limited marked population. Stable isotope markers rely on the principle that, in equilibrium situations, animal tissues reflect the isotopic structure of local foodwebs. Since isotopic patterns in foodwebs can differ spatially, the measurement of isotopic profiles in animal tissues can provide information on animal origins. Thus, animals are linked through foodwebs to underlying isoscapes. This realization has led to a renaissance of interest in describing and predicting isoscapes from local to continental scales as a means to track animal migration (West et al. 2006; Hobson and Wassenaar 2008).

13.2 The Three Principles of Isotopic Tracking

The successful use of isoscape information in animal tracking relies on some simple principles. The first is that the “isoscape terrain” through which the animal of interest moves must be known. In some cases, this can be a relatively easy criterion to meet. Some animals may simply move between biomes with different photosynthetic pathways (e.g. C3, C4, CAM) and so are exposed to foodwebs differing in isotope (especially ^{13}C and ^2H) abundance (e.g. Alisauskas et al. 1998; Wolf and Martinez del Rio 2000). Alternatively, they may move across a geological substrate that is a gradient between young and old formations that in turn represents a gradient in relative abundance of ^{87}Sr (Barnett-Johnson et al. 2008). However, in many cases, isoscapes are less well categorized and moreover, the researcher may be unaware of all *possible* isoscapes visited by the organism prior to capture.

The second principle is that isotopic values in animals can be offset from baseline isoscape values due to isotopic discrimination and such discrimination factors need to be known for the tissue of interest (Hobson and Clark 1992a). Other physiological processes should be known as well, including metabolic routing of specific macronutrients from diet to specific animal tissues, and other processes that can change tissue isotope ratios once the animal is in equilibrium with a foodweb. The third principle is that the time period of spatial integration corresponding to a particular animal tissue is known. For metabolically active tissues, the time period over which the spatial information is available will differ due to different tissue elemental turnover rates. Fast turnover tissues will represent short periods of dietary information and slow turnover tissues will represent longer periods (Hobson and Clark 1992b). For metabolically inactive tissues like feathers, hair and nail, a longitudinal isotopic record of previous origins is possible. The successful application of isoscapes to animal tracking requires, then, an understanding of baseline isoscape pattern, tissue-specific isotopic discrimination and patterns of turnover. Not all applications of the stable isotope method to tracking animal movements will meet all of these criteria. This is not to suggest that they cannot still provide useful information that might, for example, eliminate *possible* origins. However, we should

all strive to improve our understanding and consideration of these principles in future work. The following sections will address each of these components in turn.

13.3 Isoscapes

We primarily consider terrestrial and freshwater isoscapes that have potential in animal tracking studies. There is also a great deal of interest in the development of marine isoscapes in order to assist the tracking of marine mammal and fish stocks but this field is less advanced currently (but see Graham et al. 2009, this volume). The extent of the world's oceans and complexity of processes influencing baseline foodweb isotope values makes this a challenging area deserving its own treatment. We refer the interested reader to consider the detailed zooplankton marine isoscapes for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ developed for the Bering, Chukchi and Beaufort seas by Schell et al (1998) and to the use of the subtropical convergence isotopic threshold in the Southern Ocean for tracking movements of the Southern Right Whale (*Eubalaena australis*, Best and Schell 1996). Other researchers have inferred feeding origins of seabirds in the southern hemisphere based on a pronounced depletion in foodweb ^{13}C with latitude (Cherel and Hobson 2007; Quillfeldt et al. 2005). Elsewhere, researchers have broadly inferred inshore and offshore feeding of marine vertebrates based on relatively ^{13}C depleted pelagic vs. benthic marine foodwebs (Hobson et al. 1994; Reich et al. 2007). Recently, Popp et al. (2007) investigated compound-specific analyses of individual amino acids in Yellowfin Tuna (*Thunnus albacares*). That study did not address marine isoscapes per se but did reveal that it may be possible to infer marine isoscape patterns more readily by using isotopic analyses of essential amino acids of top predators since these amino acids should not be affected by trophic level and so will be more directly related to baseline source values.

13.3.1 C3/C4/CAM ($\delta^{13}\text{C}$, δD)

Isoscapes related to photosynthetic physiology of plants have received much attention and are covered in greater detail elsewhere in this book. These isoscapes involve the use of $\delta^{13}\text{C}$ measurements to distinguish C3, C4 and CAM metabolism which is, in turn, influenced largely by climatic factors and so can vary spatially across continents or with altitude. CAM plants can additionally be distinguished from C4 plants through the use of δD measurements (e.g. Wolf and Martinez del Rio 2000). Similarly, plant $\delta^{15}\text{N}$ values can be modeled based on climate variables known to influence plant metabolism but this isotope is inherently more difficult to model as an isoscape due to numerous other factors such as agriculture and anthropogenic landscape changes and modification of soils (Nadelhoffer and Fry 1994; Pardo and Nadelhoffer 2009, this volume). Additionally, because trophic position strongly influences animal tissue $\delta^{15}\text{N}$ values, placing organisms to $\delta^{15}\text{N}$ isoscapes requires a good understanding of isotopic discrimination.

Some of the earliest terrestrial studies involving the forensic use of isotopes in investigations involving animal tissues were based on the use of $\delta^{13}\text{C}$ measurements to track relative use of C3 and C4 plants. Initially, these applications dealt with archaeological investigations of the use of corn by ancient human populations in the New World (Burger and Van der Merwe 1990). The use of corn by migratory birds can also provide information on previous movements since corn-growing regions are often well known at continental scales (Alisauskas et al. 1998). The development of C4 agricultural isoscapes based on corn production (and to a lesser extent on production of other C4 crops like sorghum and sugar cane) are feasible and could be used to track those species known to use agricultural landscapes. This would be particularly useful when combined with δD measurements that could provide latitudinal information. For example, Wassenaar and Hobson (2000) showed a strong segregation between two groups of Red-winged Blackbirds (*Agelaius phoeniceus*) clearly related to corn consumption in agricultural areas and further associated those corn areas with more northern latitudes in the USA using feather δD values. Such agricultural isoscapes based on corn production might be particularly dynamic given recent interest in using corn for ethanol production in North America and so it will probably require year-specific isoscape information for any given animal tracking study of interest.

Mapping discrete distributions of C4 crops in an otherwise C3 landscape, while useful for some applications, will be generally less important than the use of isotopic gradients associated with large spatial scales. In such cases, animals of interest will be associated with more natural plant communities. In North America we generally expect an increase in $\delta^{13}\text{C}$ values in plant communities with decreasing latitude and increasing altitude (Graves et al. 2002; Hobson et al. 2003). However, in their development of a combined $\delta^{13}\text{C}$ and δD isoscape of Monarch Butterfly (*Danaus plexippus*) wing chitin for the eastern North American breeding population, Hobson et al. (1999) found that monarch wing $\delta^{13}\text{C}$ increased with latitude, a phenomenon presumably associated with the isotopic composition of host milkweed (*Asclepia* spp.). Thus, some ecological situations will clearly require the ground truthing of expected isoscape patterns.

Isoscapes modeled on the expected proportion of C3 and C4 plants across landscapes is one product of use to researchers interested in tracking migratory animals. However, enrichment in C3 plant $\delta^{13}\text{C}$ values due to mechanisms associated with water-use efficiency have also proved useful. The classic example of this was provided by Marra et al. (1998) who showed that American Redstarts (*Setophaga ruticilla*) wintering in xeric habitats in Jamaica were enriched in ^{13}C compared to those wintering in moist habitats. Such differences in habitat occupancy on the wintering grounds were connected to departure times and actual expected breeding success. This concept of seasonal interactions established through the isotopic measurement of bird tissues grown on the wintering grounds has led to great interest in using stable isotopes to infer past habitat use by migrant species (Hobson 2008; Marra et al. 2006). Further development of $\delta^{13}\text{C}$ isoscapes associated with the wintering grounds is needed as well as refinements in our understanding of how this isotope can be used to infer habitat conditions. Certainly, any $\delta^{13}\text{C}$ isoscape that models expected average plant community values due to a variety of biogeographic and physiological processes will potentially assist with animal tracking.

13.3.2 *Deuterium and ^{18}O in Precipitation and Surface Waters*

It has long been recognized that deuterium and ^{18}O abundance in precipitation in North America show a continent-wide pattern with a general gradient of relatively enriched values in the southeast to more depleted values in the northwest (Sheppard et al. 1969; Taylor 1974). These patterns, populated largely by data from the long-term International Atomic Energy Agency (IAEA) Global Network of Isotopes in Precipitation (GNIP) database are among those now described for most regions of the world (Bowen et al. 2005). While this program was never designed to create regional isoscapes for these elements, it has nonetheless by default provided the backbone for the use of such isoscapes in animal tracking. The first major linkage between the abiotic precipitation isoscapes and plant material was provided by Yapp and Epstein (1982). Cormie et al. (1994) then showed an excellent correlation between δD in deer bone collagen and average growing season precipitation δD . That work inspired Chamberlain et al. (1997) and Hobson and Wassenaar (1997) to examine how well such precipitation isotope values were passed on to birds growing feathers at known locations at a continental scale across North America. The strong correlation ($r^2 = 0.89$) measured by Hobson and Wassenaar (1997) between feather δD and the mean growing season average precipitation δD for forest songbirds across the central part of the North American continent indicated the immense potential seemingly too good to be true. Fortunately, that large-scale spatial pattern has since been confirmed by several other researchers on various avian species (Hobson 2008) as well as bats (Cryan et al. 2004).

Few measurements of $\delta^{18}\text{O}$ have been conducted on tissues of migratory organisms due primarily to the only recent developments using pyrolysis combustion allowing such measurements. However, Fourel et al. (1998) showed a strong relationship between δD and $\delta^{18}\text{O}$ for chitin in wings of Monarch Butterflies demonstrating that the meteoric relationship between these two elements can be passed on up the foodweb. This opens up the possibility of inferring environmental and spatial information by measuring both isotopes in tissues of migratory animals. Recently, Ehleringer et al. (2008) showed excellent agreement between drinking water δD and $\delta^{18}\text{O}$ measurements and those in human hair across the United States. The current challenge is that oxygen can be fixed in animal tissues through diet, air, and drinking water and it is just not clear how departures from the meteoric relationship should be interpreted. Nonetheless, heat stress in animals and evapotranspiration in local environments are expected to change the relationship between tissue δD and $\delta^{18}\text{O}$ in animal tissues and so may be useful in identifying those individuals coming from specific habitats like deserts.

13.3.3 *Strontium Isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) and the Heavy Element Advantage*

The natural variation in strontium isotopes ($^{87}\text{Sr}/^{86}\text{Sr}$) is becoming increasingly used in animal migration research, especially to track movements of fish among aquatic

ecosystems (Kennedy et al. 2002; reviewed by Rubenstein and Hobson 2004; Barnett-Johnson et al. 2008). One advantage in using a heavy isotope system to track animal movements compared to light isotopes is that there is usually negligible or no isotopic fractionation from geologic sources through foodwebs and into tissues. The lack of Sr isotope fractionation between dietary inputs and tissues has been shown for a variety of different animals and skeletal tissues including antlers from reindeer (Aberg 1995), elephant, mammoth, and mastodon bone and tusks (Vogel et al. 1990; Koch et al. 1995; Hoppe et al. 1999), marine and freshwater fish teeth, vertebrae, and otoliths (Koch et al. 1992; Kennedy et al. 1997; Ingram and Weber 1999), and human teeth and bones (Ezzo et al. 1997). For some freshwater vertebrates, such as fish, dissolved Sr in water is the primary source of Sr in tissues, although prey and water Sr sources are usually isotopically identical (for exception due to aquaculture see Ingram and Weber 1999; Walther and Thorrold 2006; Kennedy et al. 2000). Thus, the use of $^{87}\text{Sr}/^{86}\text{Sr}$ as a tracer for animal migrations has explicitly focused on identifying geographic regions that an animal has inhabited based on different regional geologies.

There are three stable isotopes of Sr: ^{88}Sr (82.53%), ^{86}Sr (9.87%), and ^{84}Sr (0.56%). The ^{87}Sr isotope of Sr (7.04%) is radiogenic and is produced by the beta decay of ^{87}Rb (half-life = 48.8×10^9 years), which contributes to the distinctly different ^{87}Sr abundances and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios across different parts of the landscape. It is well known from over three decades of geologic research that variations in $^{87}\text{Sr}/^{86}\text{Sr}$ are a function of both the age of the crust and distinctive Rb/Sr ratios in rock types. For example, rocks that are older and ones that have high Rb/Sr ratios (e.g., sandstone, shale and granites) have higher $^{87}\text{Sr}/^{86}\text{Sr}$ ratios than younger rocks or rock types with low Rb/Sr ratios (e.g., basaltic lavas, limestone, and marble; Faure 1977; Aberg 1995).

Sr isotopes are ideal markers for the development and use of isotope mapping because of the lack of biotic fractionation, well-documented geologic mechanisms creating spatial variation across the landscape, and low temporal variability (Graustein 1989; Blum et al. 2000; Kennedy et al. 2000). The only published example of a large-scale Sr isoscape models bedrock $^{87}\text{Sr}/^{86}\text{Sr}$ of the United States as a function of rock age (Beard and Johnson 2000). This approach is particularly useful for constraining the location and habitat of migrants at a large-scale. However, many studies have empirically measured $^{87}\text{Sr}/^{86}\text{Sr}$ and found significant variation on finer spatial scales largely due to variation in rock type (Kennedy et al. 1997; Hoppe et al. 1999; Barnett-Johnson et al. 2008). Not quantifying $^{87}\text{Sr}/^{86}\text{Sr}$ variation on small-scales can confound classifications and limit the utility of Sr isoscapes depending on the scale of migration of an animal.

Several characteristics of $^{87}\text{Sr}/^{86}\text{Sr}$ incorporation and analyses may limit its broad use across taxa (reviewed by Wassenaar 2008). Sr occurs at low concentrations in non calcium-bearing tissues like bird feathers ($<20 \mu\text{g Sr/g}$) and requires costly and extensive wet chemistry to isolate Sr for isotopic analyses typically on a thermal ionization mass spectrometer (TIMS; Kennedy et al. 1997; Font et al. 2007). These constraints have limited their use over light isotopes in bird migration research. In contrast, Sr occurs in much higher concentrations (e.g., $>$ ten times that of feathers)

in bony tissues (e.g., teeth, bones, otoliths) and is growing in use in fish migration research, wildlife forensics (e.g., deer), and human migration applications (Beard and Johnson 2000). Kennedy et al. (1997) found that different bony tissues within individual juvenile Atlantic salmon (*Salmo salar*) in a river have the same Sr isotopic values (e.g., otoliths, vertebrae), although overall Sr/Ca may vary and turn-over rates for different tissue types may need to be considered once individuals migrate into areas characterized by different $^{87}\text{Sr}/^{86}\text{Sr}$ sources.

Recent advancements in analytical instrumentations have contributed to the elevation of $^{87}\text{Sr}/^{86}\text{Sr}$ from a specialized assay to large sample size applications (Hobbs et al. 2005; Walther and Thorrold 2008). Precise measurements of $^{87}\text{Sr}/^{86}\text{Sr}$ can be achieved with multi-collector inductively coupled plasma mass-spectrometry (MC-ICPMS) in geologic and biologic samples thereby significantly decreasing analytical costs, increasing sample throughput and eliminating the need for extensive wet chemistry (Ramos et al. 2004). In addition several new applications in fisheries science can be pursued because of laser ablation capabilities with MC-ICPMS which allow reconstructions of fish migrations from the daily growth rings recorded in otoliths at high temporal resolutions of movement (e.g., 10 days; Barnett-Johnson et al. 2005; Woodhead et al. 2005).

13.4 Isotopic Discrimination and Physiological Considerations

For many elements, only slight changes in stable isotope ratios occur between trophic levels after they are fixed by plant tissues. Isotopes of sulfur and possibly hydrogen fall into this category along with the heavier elements like Sr. While overall ^{13}C discrimination between diet and the whole body of animals is relatively small (i.e. of the order of 1‰), tissues differ in the amount of isotopic discrimination and absolute values for keratinous tissues can be significant. Trophic discrimination associated with ^{15}N is substantial (of the order of 3.4‰; Post 2002) and has been used as a trophic indicator. Relating animal tissues to ^{15}N isoscapes will therefore require careful consideration of the trophic level of the animal of interest. Also, stable nitrogen isotopes in the tissues of consumers really represent a means of tracing protein pathways derived from diet since this element is largely absent in lipids and carbohydrates. For essential amino acids, nitrogen will largely be incorporated with little isotopic discrimination into the protein pool of the consumer. Non-essential amino acids typically involve more opportunities for isotopic discrimination during protein synthesis and so the net discrimination we see for $\delta^{15}\text{N}$ measurements in consumers will reflect the degree to which the diet meets the amino acid requirement of the consumer (Robbins et al. 2005). Isotopic discrimination associated with $\delta^{15}\text{N}$ will also depend on the means of voiding nitrogenous waste. Here, a major difference is found between aquatic invertebrates that void nitrogen via ammonia compared to terrestrial vertebrates (Post 2002). Hobson et al. (1993) also determined that birds that fast and undergo significant protein catabolism during incubation, like geese breeding at high latitudes, also experience an increase in body $\delta^{15}\text{N}$

values. Knowledge of these sorts of physiological processes is necessary, then, when using tissue $\delta^{15}\text{N}$ values of migratory organisms to infer origins. The current consensus is that researchers should strive to use the most parsimonious value associated with their specific organism of interest. The review of isotopic discrimination in $\delta^{15}\text{N}$ across several taxa by Vanderklift and Ponsard (2003) identified mode of excretion and environment (marine, freshwater aquatic, terrestrial) as important factors (see also Post 2002).

Isoscapes of ^{15}N for use in tracking migratory animals are complicated by the fact that ^{15}N in foodwebs can be influenced by several factors, not the least of which is the trophic level of the target individual or species. Plant ^{15}N is influenced by the mode of nitrogen fixation but also by ambient temperature and moisture. In addition, anthropogenic influences such as land clearing and use of fertilizer influence plant $\delta^{15}\text{N}$ values (Pardo and Nadelhoffer 2009, this volume).

13.5 Isotopic Turnover

The concept of isotopic turnover in animal tissues is fundamental to understanding how stable isotope values can be interpreted as a temporal record of past movements. Such information, together with an understanding of the isotopic differences between isoscapes used by individuals can define the statistical power of inference applicable to a particular question of tracking (Hobson 2008). The larger the isotopic difference between any two isoscapes and the slower the turnover in tissues of interest, the greater the time over which previous use of one isotope over the other can be detected. Previous researchers have attempted to experimentally derive isotopic turnover using diet-switch experiments. Recently, this field has received more attention as different ways of interpreting patterns of isotopic turnover in animals have been explored. These include a move away from fitting a simple exponential decay function to the data. These new approaches have identified that in some situations more than one nutrient pool is involved in tissue synthesis and this has important ramifications for tracking migrants.

A first order rate constant is:

$$\frac{dN}{dt} = -\lambda N \quad (13.1)$$

where N is the number of atoms or molecules in the system being described, t is time (s), and λ is the rate constant (s^{-1}). Integrated, this is:

$$N = N_0 e^{-\lambda t} \quad (13.2)$$

For isotope ratios, this is analogous to:

$$\frac{R_A^t - R_A^{eq}}{R_A^{init} - R_A^{eq}} = e^{-\lambda t} \quad (13.3)$$

where R_A^{init} is the initial isotope ratio ($t = 0$), R_A^{eq} is the isotope ratio at equilibrium ($t = \text{infinity}$), and R_A^t is the isotope ratio at time t , respectively. Using the δ -notation, this becomes:

$$\frac{\delta_A^t - \delta_A^{eq}}{\delta_A^{init} - \delta_A^{eq}} = e^{-\lambda t} \quad (13.4)$$

multiple components that contribute to the system

By treating the system as having first-order reaction kinetics, it is often possible to resolve multiple components that contribute to the system. Experiments designed to derive turnover rate constants usually involve a diet or water “switch” from the initial conditions to those with a very different isotope ratio. Recent work has shown that some tissues exhibit “multiple turnover pools” (e.g., hair, liver, or muscle; Ayliffe et al. 2004; Zazzo et al. 2007; Sponheimer et al. 2006; Martinez del Rio and Anderson-Sprecher 2008) whereas other body tissues or fluids exhibit only one turnover pool (e.g., blood plasma, red blood cells, bodywater/breath; Podlesak et al. 2008). Many experiments have not been designed to identify multiple pools, in part because of the difficulty in obtaining many samples immediately following a diet or water switch and more fundamentally because a single exponential decay function was assumed to adequately fit the data; we expect that this will change in the next decade as experiments are designed to detect multiple turnover pools. Likewise, compound specific analyses may show that individual components of tissue may have different turnover rates (e.g., essential versus non-essential amino acids).

The understanding of isotope turnover is particularly useful in interpreting dietary histories from sequential samples. This can help place an individual on an “isotope” at a particular time, or can otherwise show changes in diet or water resource use. For a first-order reaction, each isotope pool changes with time as (from Cerling et al. 2007):

$$\delta_j^t = \delta_j^{(t-1)} e^{-\lambda_j(\Delta t)} + \delta^{eq} (1 - e^{-\lambda_j(\Delta t)}) \quad (13.5)$$

where $\delta_j^{(t-1)}$ is the isotope value of pool j at time $(t - 1)$, and Δt is the difference in time between “ $t - 1$ ” and “ t ”. For a change in isotope input value, the isotope value δ_j^t can be calculated as a function of time using this equation if δ^{eq} is known. For the case where the δ^{eq} can be related to a known fractionation factor α , a dietary history can be reconstructed from a sequence of hair samples by (Cerling et al. 2007). The following equation is for the case of three isotope turnover pools:

$$\delta_D^{(t)} = \frac{\left(\frac{\delta_H^{(t)} + 1000}{\alpha_{HD}} - 1000 \right) - \left(\sum_{j=1}^3 f_j \delta_j^{t-1} e^{-\lambda_j \Delta t} \right)}{\left(\sum_{j=1}^3 f_j (1 - e^{-\lambda_j \Delta t}) \right)} \quad (13.6)$$

where $\delta_D^{(t)}$ is the isotopic composition of diet at time “ t ”, $\delta_H^{(t)}$ is the isotopic composition of an individual hair segment in a sequence of hair samples at time “ t ”, α_{HD} is the isotope fractionation factor between tissue and diet (written as enrichment), f_j is the fractional contribution of each isotope turnover pool, $\delta_j^{(t-1)}$ is the isotope composition of the hair segment older than the one being measured ($t - 1$), and Δt is the difference in time between segment “ i ” and segment “ $i, t - 1$ ”. In this analysis it is often the case that the shortest turnover pools equilibrate very rapidly (within one or two sampling intervals) whereas the longest turnover pools never reach equilibrium; therefore it is necessary to make a best “guess” for the isotopic composition of the longest pool: Cerling et al (2007) suggest that the long term average value for that pool is appropriate unless other knowledge of the dietary history is known.

How important is the detailed knowledge of the various fractional contributions and the values of the various turnover pools? Is a “close approximation” good enough for “isoscapes location?” We provide an example that compares several different models for turnover times of two pools. For the case of hair, various research groups have found that multiple pools contribute to the isotopic composition of carbon in hair: in particular they find that there is one (or more) pool(s) with a half-life of a few days or less, and a pool that is much longer. Further, most groups have found that these contributions are subequal (between the proportions 70/30 and 50/50). Ayliffe et al (2004), Zazzo et al. (2007), and Podlesak et al. (2008) found the long pool to have half-lives of ca. 140, 70, and 140 days for horses, cows, and woodrats, respectively. The half-lives and turnover of ^{15}N is not known for these studies because none of them had a large enough $\delta^{15}\text{N}$ difference in the starting and final conditions; however, the observed isotope enrichment for most herbivorous mammals is ca. 3‰ for normal or poor-protein diets (i.e., excluding high protein diets; Sponheimer et al. 2006). We model the diet input for an individual elephant (*Loxodonta africana*) known to occupy two regions: semi-arid bushland to montane forest (Cerling et al. 2006). We calculate the diet as described above for four models: one is the instantaneous equilibrium with the environment ($t_{1/2} < 2$ days for all pools), and three models with a short half-life (< 2 days) and a long half life (70, 100, or 140 days, respectively). All models use equal contributions (50:50). Figure 13.1 shows calculated diets for the four different models given above; it is evident that for this case, what is important is that both “long” and “short” pools exist but that the absolute half-lives of the “long” pools are relatively unimportant.

The individual elephant occupied two regions, spending most of his time in one region with short “expeditions” to another region where he resides, at most, a few months a year. Tracking the isotope composition of the “long” and “short” pools shows that the “short” pool is always in equilibrium with the local environment, while the long pool is strongly dominated by the long-term resident environment and that the relatively short visits to the new environment are not long enough to change the isotopic ratio of the “long” pool. The net result of this is that all models, including instantaneous equilibrium with the environment, predict a similar diet for the region where the individual spends most of his time; however, the “instantaneous” equilibrium model predicts a different environment than all dual-pool models

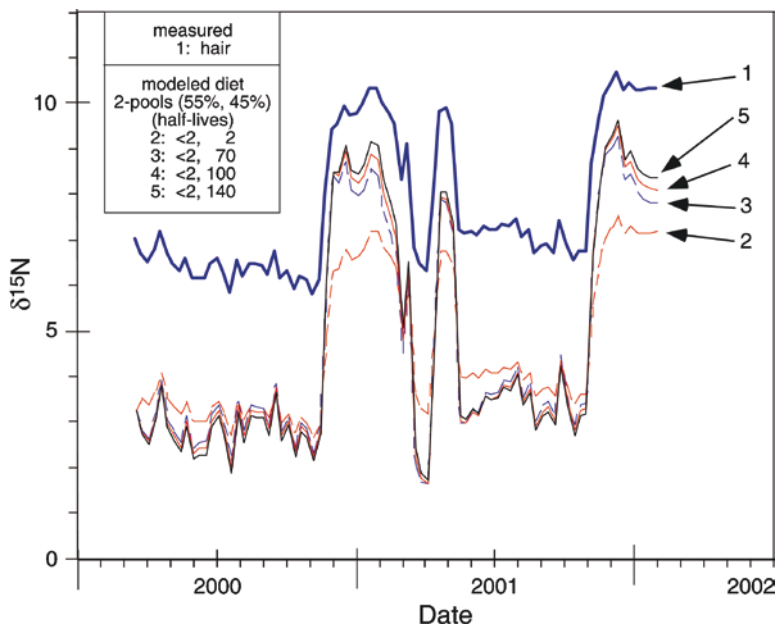


Fig. 13.1 Measured hair values from a migrating African elephant and modeled diets using the 2-pool model described in text. Migration was from a region of high $\delta^{15}\text{N}$ values to one of low $\delta^{15}\text{N}$ values; transit time between the regions was less than 12 h based on GPS observations (Cerling et al. 2006). Model results are for “one-pool” (all half-lives less than sampling interval), and three scenarios where the long pool had 50% contribution but half-lives of 70, 100, and 140 days, respectively. This sensitivity study shows that the multiple pool model is different than the single pool model, but that the length of the long pool is less important than the fact that there are two pools present. Fig. 13.1, see Appendix 1, Color Section

which do not differ substantially. This exercise illustrates that the “apparent” enrichment between diet and tissues is different in the different environments, and that this is a result of a non-equilibrium condition where the long turnover times for one of the pools contributes differentially to the tissue being studied. Clearly, appropriate models should be used to determine the environmental “isoscapes” occupied during migration of animals. Fortunately, however, this model shows that the exact parameters of all models do not have to be determined in all cases to make good estimates of the environmental history of individuals.

13.6 Some Key Case Studies

13.6.1 *Birds and Insects*

Bird feathers and insect wing chitin are two very useful materials for isotopic tracking of movements because they are essentially inert following formation and so provide information on origin during the relatively short period of formation.

Once considerations of the importance of single vs. multiple pool nutrient sources are resolved (and it has generally been assumed but rarely shown explicitly that bird feathers overwhelmingly reflect diet during feather growth, but see Fox et al. 2009) the molt phenology, and hence choice of feather for analysis, of a particular species will be crucial to interpretation. Unfortunately and somewhat surprisingly, molt phenology is often not well understood for all species, particularly at the population or sub-species level and some researchers have confused problems with isotope data and problems with their understanding of molt (Larson and Hobson 2009). However, when details of molt are known, researchers have been able to use more than one feather type per individual to infer origins at different periods of the annual cycle (Mazerolle and Hobson 2005). Similar arguments apply to periods of hair growth in mammals (Britzke et al. 2009).

The first true animal isoscape was produced by Hobson et al. (1999) who investigated where Monarch Butterflies that wintered in Mexico originated in their eastern North American breeding areas. That study created an isotopic basemap or isoscape corresponding to δD and $\delta^{13}\text{C}$ values in butterfly wing chitin. Interestingly, that isoscape was produced with the help of 80 elementary schools across the range. Young students raised butterflies from eggs on host milkweed plants in gardens receiving only natural precipitation. Wing chitin isotope values were then measured from 1,300 individuals collected at all known roost sites in Mexico the winter following the creation of the isoscape (i.e. corresponding directly to the production year of interest). So, these authors created the δD and $\delta^{13}\text{C}$ isoscape relevant to the period of interest. Since this isoscape was based on the actual tissue measured (i.e. wing chitin) no correction was required linking abiotic or foodweb isotope values to butterfly wing isotope values. This approach, although laborious, satisfied the three principles of tracking using isoscapes. Unfortunately, the creation of a species-specific tissue isoscapes for the year of interest is beyond the realm of possibility for most applications.

Since then, relatively few studies have used stable isotopes to track migratory insects (but see Brattström et al. 2008) despite the fact that a great deal of potential exists for this taxon. One complicating variable with insects is that many species of interest are agricultural pests and originate in cropland that has been irrigated with groundwater. This potentially undermines the use of the water isoscape products based primarily on the GNIP precipitation dataset.

The greatest advances in using isoscapes to track migration has been those concerned with birds and chiefly using the continental deuterium in precipitation patterns. Two key papers are noteworthy. The first by Kelly et al. (2002) showed that western North American populations of Wilson's Warbler (*Wilsonia pusillus*) undergo a leapfrog migration to their wintering grounds in Central America whereby more northern breeding populations fly over more southern populations to winter the furthest south. The other study involved an establishment of migratory connectivity between breeding and wintering grounds of Black-throated Blue Warblers (*Dendroica caerulescens*). In that study, Rubenstein et al. (2002) also made use of a longitudinal gradient in feather $\delta^{13}\text{C}$ values to better delineate origins. These studies were important because they represented insights into the migratory connectivity of

these populations that simply could not be achieved without the use of stable isotope measurements and an *a priori* knowledge of isoscape pattern. However, neither study attempted to provide a rigorous statistical treatment of the confidence of assignment of individuals and this remains an area of much needed development (see below).

In an extensive analysis of over 700 individuals taken throughout the autumn migratory central flyway in North America, Hobson et al. (2006) delineated origins of both adult and young-of-the-year Sandhill Cranes (*Grus canadensis*). That study revealed that the region with greatest production of young contributing to the flyway differed spatially from the area from which adult birds were derived (Fig. 13.2). This result has profound consequences for the management of this species. The approach used by Hobson et al. (2006) in that and other studies (Wassenaar and Hobson 2001a; Hobson et al. 2007) was to consider a fixed discrimination factor between the deuterium growing season average precipitation isoscape and feathers and use this in an additive fashion in GIS to produce a feather δD isoscape. That discrimination factor was derived from previous experimental and observational studies and reinforced from analysis of regression results of modeled precipitation and measured feather δD values (Hobson 2008). They then delineated those regions on the feather isoscape corresponding only to the breeding distribution of this species and then further depicted origins as falling within isocontours defined by percentiles (Fig. 13.2). That approach is straightforward and has considerable appeal. However, the approach does not propagate error associated with our estimate of a precipitation to feather discrimination. Hobson et al. (2006) performed a sensitivity analysis on their results to determine the effect of altering their discrimination factor by $\pm 5\%$ but more advanced statistical approaches are now possible to propagate error associated with tissue isoscapes and, more appropriately, to depict probability of origin surfaces (Wunder and Norris 2008).

13.6.2 Mammals

Like bird feathers and claws or whale baleen plates, animal hair, claws and hooves can provide an isotopic chronology of past movements, diets, and biomes (Barnett 1994; Drucker et al. 2008). Sequential sampling of such tissues holds great promise when combined with knowledge of isoscape patterns encountered by migratory mammals. These studies will be enhanced by investigations of tissue growth rates and how these change seasonally and with diet quality.

There has been considerable interest in using isoscapes to infer previous origins of mammals. An early seminal study involving Bowhead Whale (*Balaena mysticetus*) migration from the Beaufort to the Bering Chukchi seas using $\delta^{13}C$ and $\delta^{15}N$ measurements of the baleen plates of these animals (Schell et al. 1988). That study was also based on a clear understanding of the marine isoscape through which whales moved (see Schell et al. 1998). More recently, other isotopes and trace elements have been used to see how well they correlate with annual movements of western

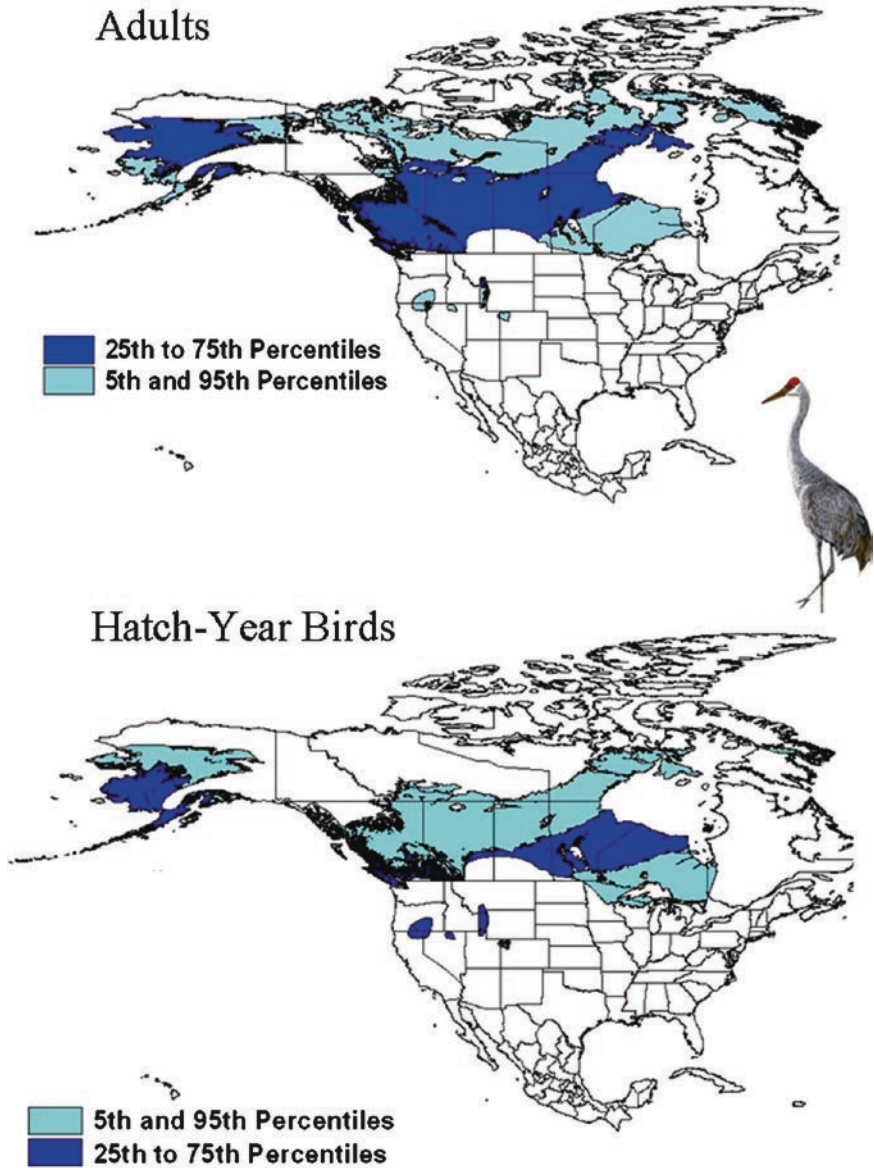


Fig. 13.2 Depictions of the origins of adult and young-of-the-year Sandhill Cranes based on the distributions of their feather δD values and the use of a feather δD isoscape in turn derived primarily from the GNIP database. This figure illustrates one means of depicting origins of migratory organisms without error propagation. Results are based on Hobson et al. (2006) who examined over 700 individuals harvested by hunters in the Central Flyway and provide important conservation information on where most young were produced. Fig. 13.2, see Appendix 1, Color Section

Bowhead Whales. Hobson and Morrison examined δD values along the plate of a Western Bowhead Whale taken in the Beaufort Sea region of western Canada. That individual showed characteristic oscillations in baleen δD consistent with its annual migration between relatively deuterium depleted waters of the Beaufort to the more enriched values of the Bering and Chukchi seas where these whales winter (Fig. 13.3). A positive drift in baleen δD values between more recent and older portions of the baleen may have been due to increased freshwater input from the Mackenzie River in more recent times but that remains to be tested. Importantly, this example illustrates that isotopic baselines associated with isoscape patterns may change due to biotic and abiotic processes (see also Cullen et al. 2001; Schell 2001). We suspect that δD and $\delta^{18}O$ measurements may be useful markers at high latitudes in marine systems.

In terrestrial applications, early attempts to trace origins of African ivory using isotopes of light and heavy elements based on measured values of source populations at specific reserves or national parks did not involve the use of isoscapes *per se* but did rely on isotopically defined source populations. That approach is also amenable to the use of trace element analyses (Szép et al. 2003) because populations of interest can be typed or categorized since baseline values, in turn determined by soils or geological substrates, are expected to remain relatively unchanged.

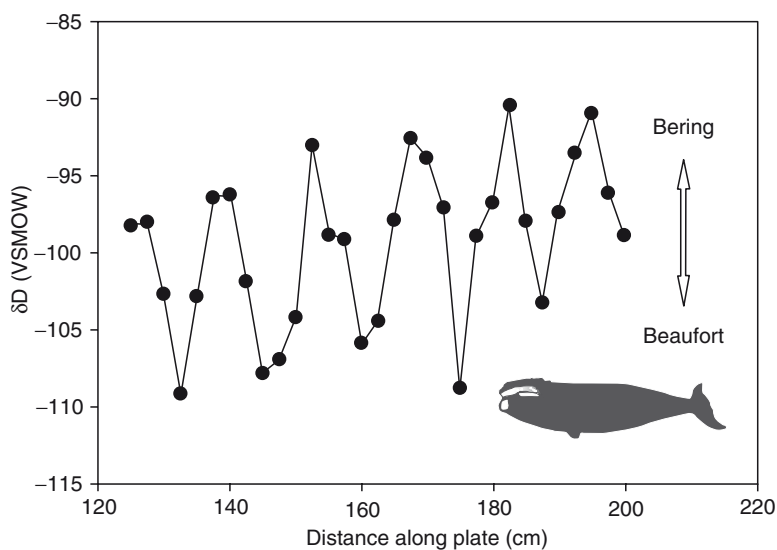


Fig. 13.3 Baleen δD values from a western Bowhead Whale annually moving between the eastern Beaufort and the Bering and Chukchi seas. This illustrates that high-latitude marine isoscapes are a possible resource for tracking migratory marine mammals and fish

Cormie et al. (1994) was the first to associate bone collagen δD values of deer to those expected from the mean growing season average precipitation surface. Since then, relatively few applications to questions of terrestrial animal migration have been conducted although Cerling et al. (2006) have continued to look at individual movements of animals relative to expected or measured isoscapes. An exception has been the investigation of Cryan et al. (2004) who derived a regression between hair δD values of bats and the precipitation δD isoscape for North America. That study should encourage further use of a bat hair δD isoscape to infer origins (e.g. Britzke et al. 2009). One of the fundamental problems with the application of the stable isotope tracking technique to bats is that their hair growth periods are often poorly understood and their ability to revert to torpor and their active mobilization of body nutrients during lactation renders them a problematic group.

13.6.3 Fish

Otoliths are structures in the inner ears of fishes which grow by the daily deposition of calcium carbonate and protein layers throughout the life of a fish. Elements (e.g., Sr) in the surrounding waters substitute for calcium and get incorporated into the fish otolith. Since otoliths are metabolically inert, their isotopic composition can provide a permanent chronology of different water masses or habitats occupied by a fish and are ideal structures for reconstructing movement patterns.

Sr isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) ratios in otoliths are powerful tools to address fundamental questions in fish ecology, conservation, and fisheries management. $^{87}\text{Sr}/^{86}\text{Sr}$ in otoliths have been used to identify natal freshwater habitats (Kennedy et al. 1997; Ingram and Weber 1999; Barnett-Johnson et al. 2008), track small-scale freshwater movement patterns (Kennedy et al. 2000), and chronicle timing of migration between marine and freshwater environments (Koch et al. 1992; Bacon et al. 2004; McCulloch et al. 2005). Kennedy et al. (1997) first demonstrated the potential of using $^{87}\text{Sr}/^{86}\text{Sr}$ measurements to identify key production rivers contributing to the adult population of Atlantic salmon. Their work showed that the water in the majority of rearing streams for Atlantic salmon in the Connecticut River differed significantly in their $^{87}\text{Sr}/^{86}\text{Sr}$ signatures, based on watershed geology and the same isotopic values were transferred to fish tissues (Fig. 13.4). This work inspired the application of $^{87}\text{Sr}/^{86}\text{Sr}$ in otoliths to track other species of anadromous and freshwater fishes in different systems.

The recent advancement of analytical instrumentation using laser ablation MC-ICPMS allows spatial coordination of $^{87}\text{Sr}/^{86}\text{Sr}$ measurements in the daily growth rings recorded in otoliths. This allows reconstruction of fish migrations through geochronology at high resolutions and high sample throughput necessary for many fisheries applications. Using this analytical breakthrough, Barnett-Johnson (2007) was able to conduct a mixed-stock analysis and link the natal identity of Chinook salmon *Oncorhynchus tshawytscha* caught off the central California coast to their

rivers and hatcheries of origin in California's Central Valley. They found that only 10% ($\pm 6\%$) of Chinook salmon were from wild sources with a single hatchery largely supporting the fishery, suggesting that hatchery supplementation may be playing a greater role than previously thought. Walther and Thorrold (2008) found that American shad (*Alosa sapidissima*) returning to spawn in the York River were homing to their natal river, but that there was much less fidelity to individual tributaries. By reconstructing natal $^{87}\text{Sr}/^{86}\text{Sr}$ and Sr/Ca in adult otoliths, they found that small-scale straying could allow fish from the Mattaponi River to subsidize spawning in the Pamunkey River, which has experienced persistent recruitment failure. Here, we compile for the first time empirical measures of $^{87}\text{Sr}/^{86}\text{Sr}$ from three key fish studies to create an aquatic-focused Sr isoscape from Kennedy et al. (2000), Barnett-Johnson et al. (2008), and Walther and Thorrold (2008). These studies were chosen to provide empirical measures of $^{87}\text{Sr}/^{86}\text{Sr}$ in natal tributaries for different fish species on small and coast-wide scales for the east and west coast of the United States to highlight the utility of Sr isoscapes for fisheries applications. These empirical values from water and/or fish otoliths are placed within the context of a baseline U.S. continental-scale map with predicted $^{87}\text{Sr}/^{86}\text{Sr}$ developed by Beard and Johnson (2000) (Fig. 13.4).

The baseline map highlights first-order Sr variations ($\epsilon^{87}\text{Sr}$) inferred by age variations in basement rocks (Beard and Johnson 2000). Empirical measures of $^{87}\text{Sr}/^{86}\text{Sr}$ from the key fish studies are extrapolated to the scale of watersheds, as the $^{87}\text{Sr}/^{86}\text{Sr}$ values in otoliths and water are likely influenced by geology at this scale (Barnett-Johnson et al. 2008).

The small-scale variations in $^{87}\text{Sr}/^{86}\text{Sr}$ among rivers (e.g., natal sites) captured by empirical measurements have been used to track natal origins in a variety of fish species and systems. In California's Central Valley, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios and daily growth bands recorded in otoliths of Chinook salmon from all major natural and hatchery spawning sites can be used to identify river and hatchery of origin of Central Valley fall-run adults in the ocean with high accuracy (94–98%; Fig. 13.4a; Barnett-Johnson et al. 2008). The north to south isotopic gradient is driven by young volcanic rocks influencing watershed values in the northern part of the Central Valley river system and older granitic rocks, which predominate in the south. Along the east coast of the United States, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios vary among natal rivers for American shad across their spawning distribution (Fig. 13.4b; Walther and Thorrold 2008). Atlantic salmon in the White River in Vermont can be identified to tributary of origin by using $^{87}\text{Sr}/^{86}\text{Sr}$ and ^{15}N variation reflecting differences in geologic and agricultural inputs into salmon streams (Fig. 13.4c; Kennedy et al. 2000).

While geologic age used by Beard and Johnson (2000) explains some observed variation in measured isotopic values, there is significant disagreement between predicted and measured values (Fig. 13.4). For example, several tributaries off the Sacramento River in California have measured values of $^{87}\text{Sr}/^{86}\text{Sr}$ that are lower than any values predicted by the analysis conducted by Beard and Johnson (2000). This disagreement between observed and predicted values is likely explained by the role that lithology plays in Sr geochemistry that remains unquantified in the Beard and Johnson model and is an area primed for future research. By placing spatial variation in Sr isotope ratios in the context of bedrock geology, a mechanistic and

quantitative framework can be developed to determine how particular rock types contribute to patterns of $^{87}\text{Sr}/^{86}\text{Sr}$ variability in watersheds and otoliths. Developing these geologic models to inform Sr isoscapes across systems will assist in evaluating whether general characteristics in geology (in addition to age) emerge in explaining $^{87}\text{Sr}/^{86}\text{Sr}$ variability in otoliths and aid in forecasting the efficacy of Sr isotopes as natural tags of origin.

13.7 Current Limitations and Future Research

With few exceptions (e.g. Hobson et al. 1999; Barnett-Johnson et al. 2008), terrestrial isoscapes have not typically been created for the purposes of tracking migratory animals. Rather, ecologists and wildlife managers have made use of isotopic patterns derived for other purposes, especially those related to expected patterns based on plant physiology or long-term precipitation datasets. Ideally, available isoscapes would include those for each species and tissue of interest and include a spatial resolution appropriate to the movement patterns of the organism of interest ranging from local to continental scales. This requires huge effort and expense and so, in the near term then, we will continue to infer movement patterns of animals based on imperfect isoscape information.

Another problem with current isoscape models is that they are static and it is usually unclear just how much variance is associated with baseline or foodweb isoscapes used by animals at any particular location. While this can be accommodated to some degree by defining isotopic variance, based on long-term datasets, those data are typically unavailable for a number of isotopes. Such retrospective analyses of variance also are not particularly useful if future climatic conditions escape the natural range of variability and this in particular presents a challenge for the long-term GNIP precipitation dataset for δD and $\delta^{18}\text{O}$ measurements. Ideally, isoscapes based on the GNIP dataset and the associated variance surface would be updated annually and be flexible enough to accommodate additional sampling. Farmer et al. (2008) recently analyzed GNIP data for selected stations and years for sites in North America and Europe. They then used these estimates of variance to derive so-called fundamental limits to the resolution of origins of migratory birds using the feather δD approach. Unfortunately, those authors failed to realize that the predicted feather δD value from the long-term GNIP record refers to precipitation-weighted growing season averages and is not based on raw GNIP data. Their exercise should be repeated using the correct weighting approach. However, of more use will be regional analyses that attempt to explain the source of variance in the GNIP (or GNIP supplemented with other precipitation data sources) dataset. So, the influence of departures in precipitation amount from the long-term average and other meteorological data on the measured precipitation δD values will allow us to potentially account for departures from the web-based models of Bowen et al. (2005). Some authors are now carefully considering factors which contribute to departures in feather δD from long-term modeled averages (e.g. Coulton et al. 2009).

This research is urgently needed in regions of the continent where variance in weather patterns from long-term averages are most pronounced (e.g. the Great Plains of North America).

For isotopes such as ^{13}C and ^{15}N , recent advances in the potential for using remote sensing data to refine isoscape models presents an intriguing possibility of deriving annual isoscape models. Of course, for the heavier isotopes like those of Sr linked to geological substrates and presumed small temporal variability, the possibility exists for the establishment of relatively permanent isoscapes following some concerted effort of ground truthing. Developing a Sr isoscape in aquatic systems based on water sampling in defined watersheds and streams is feasible for fish movement and production studies since there is no significant fractionation between water $^{87}\text{Sr}/^{86}\text{Sr}$ values and otoliths in fish, as long as prey sources are in equilibrium with water. The need for modeling error propagation in assigning regions of origin for individuals across years using Sr isotopes will be dictated by the extent to which temporal variability confounds spatial differences in $^{87}\text{Sr}/^{86}\text{Sr}$ values.

For a number of animal tracking applications, the precipitation δD and $\delta^{18}\text{O}$ isoscapes will be the most useful. This suggests that particular effort be placed on refining the use of these isotopes. Apart from encouraging further analyses of the long-term GNIP dataset and refining our understanding of similar surface water datasets, much more research is needed to understand mechanisms of isotopic discrimination between foodwebs and animal tissues of interest. It seems clear that a single precipitation to tissue isotopic discrimination factor for animal δD (and presumably $\delta^{18}\text{O}$) is not appropriate. Currently, the influence of thermoregulation and work on the hydrogen isotope budget in animals and how this influences animal tissue δD values is much needed for several taxa. Fortunately, such investigations are amenable to controlled laboratory studies (McKechnie et al. 2004). Measurement of δD in animal tissues is also more complicated than the other light isotopes due to exchange with ambient laboratory water vapor due to weak N–H and O–H bonds. Wassenaar and Hobson (2003; 2006) discuss this issue at length and urge isotopists to adopt means of reporting δD values in animal tissues using a comparative equilibration technique so that data can be readily compared among laboratories. As we refine applications of $\delta^{18}\text{O}$ measurements, similar concerns are appropriate since there are currently no international standards available for $\delta^{18}\text{O}$ in organics.

The development of a Sr isoscape is in its infancy relative to light-isotope mapping for animal tracking efforts on continental scales. As such, there are several avenues for refinement and future research. A significant advancement will be to derive a quantitative geologic model that incorporates both age and rock type into $^{87}\text{Sr}/^{86}\text{Sr}$ predictions that could be scaled to both large and fine-scale resolutions. Barnett-Johnson et al. 2008 was successful at explaining 95% of the $^{87}\text{Sr}/^{86}\text{Sr}$ variation in salmon otoliths across watersheds in California's Central Valley by measuring the area of a watershed comprised of granitic rocks. However, in this system, both rock type and age co-varied so a quantitative assessment of the influence of age and lithology could not be accounted for independently. The ability to accurately characterize *unsampled* areas through the use of a geologic proxy would go far in fulfilling the first principle in an ideal isoscape. In practice, the relationship between geology

and empirical measures of $^{87}\text{Sr}/^{86}\text{Sr}$ may be challenging to model on a large-scale. For example, sedimentary rocks may contain multiple age and lithologic components and weathering rates differ among rock types. Similarly, local-scale phenomena may be necessary to consider in areas where atmospheric deposition plays a significant role in Sr addition from dust with different $^{87}\text{Sr}/^{86}\text{Sr}$ than local bedrock.

Further refinement may be necessary in the art of graphically mapping $^{87}\text{Sr}/^{86}\text{Sr}$ variation in aquatic systems. Unlike light-isotope mapping of abiotic processes where an interpolation algorithm can be used to represent neighboring areas that have not been explicitly sampled, a successful Sr isoscape will need to incorporate geologic variations that may occur on relatively small spatial scales. One current challenge is in determining the best way to display $^{87}\text{Sr}/^{86}\text{Sr}$ for rivers. The approach taken in this chapter extrapolates measured values of water [and fish] at the scale of a watershed. However, $^{87}\text{Sr}/^{86}\text{Sr}$ can vary within a river from headwaters to downstream sources and especially at the confluence with rivers characterized by different $^{87}\text{Sr}/^{86}\text{Sr}$ values (Weber 2002). This form of isotopic variation for rivers is difficult to represent graphically and needs further development.

Finally, more development is required to formulate standard protocols for depicting origins of animals based on isoscapes. Ideally, such approaches will be amenable to web-based tools and well-defined algorithms. Wunder and Norris (2008) have advocated approaches which more honestly incorporate error propagation and the ultimate derivation of probability of origin surfaces. However, much more work is required on this front to make these techniques more accessible to researchers and to test the consequences of depicting origins using a variety of GIS and spatial statistical methods. Currently, this remains as one of the biggest frontiers to the field of isotopic tracking of migratory organisms (Kelly et al. 2008).

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References

- Aberg G (1995) The use of natural strontium isotopes as tracers in environmental studies. *Water Air Soil Poll* 79:309–322
- Alisauskas RT, Klaas EE, Hobson KA, Ankney CD (1998) Stable-carbon isotopes support use of adventitious color to discern winter origins of lesser snow geese. *J Field-Ornith* 69:262–268
- Ayliffe LK, Cerling TE, Robinson T, West AG, Sponheimer M, Passey BH, Hammer J, Roeder B, Dearing MD, Ehleringer JR (2004) Turnover of carbon isotopes in tail hair and breath CO_2 of horses fed an isotopically varied diet. *Oecologia* 139:11–22
- Bacon CR, Weber PK, Larson KA, Reisenbichler R, Fitzpatrick JA, Wooden JL (2004) Migration and rearing histories of chinook salmon (*Oncorhynchus tshawytscha*) determined by ion microprobe Sr isotope and Sr:Ca transects of otoliths. *Can J Fish Aquat Sci* 61:2425–2439
- Barnett BA (1994) Carbon and nitrogen ratios of caribou tissues, vascular plants, and lichens from Northern Alaska. M.Sc. Dissertation, University of Alaska

- Barnett-Johnson R (2007) Spatial scales of mixing and natal source contributions of salmon populations in the coastal ocean detected by otolith and genetic signatures of origin. Ph.D. Dissertation, University of California, Santa Cruz
- Barnett-Johnson R, Ramos FC, Grimes CB, MacFarlane RB (2005) Validation of Sr isotopes in otoliths by laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS): opening avenues in fisheries science applications. *Can J Fish Aquat Sci* 62:2425–2430
- Barnett-Johnson R, Ramos FC, Pearson T, Grimes CB, MacFarlane RB (2008) Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. *Limnol Oceanog* 53:1633–1642
- Beard BL, Johnson CM (2000) Strontium isotope composition of skeletal material can determine the birth place and geographic mobility of humans and animals. *J Forens Sci* 45: 1049–1061
- Best PB, Schell DM (1996) Stable isotopes in Southern Right Whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Mar Biol* 124:483–494
- Blum JD, Taliaferro EJ, Weisse MT, Holmes RT (2000) Changes in the Sr:Ca, Ba:Ca, and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios between trophic levels in two forested ecosystems in the northeastern, USA. *Biogeochem* 49:87–101
- Bowen GJ, Wassenaar LI, Hobson KA (2005) Application of stable hydrogen and oxygen isotopes to wildlife forensic investigations at global scales. *Oecologia* 143:337–348
- Brattström O, Wassenaar LI, Hobson KA, Åkesson S (2008) Placing butterflies on the map – testing resolution of three stable isotopes within Sweden using the monophagous peacock *Inachis io*. *Ecography* 31:490–498
- Britzke ER, Loeb SC, Hobson KA, Romanek CS, Vonhof, MJ (2009) Assessing origins of bats using stable hydrogen isotope analysis: an investigation of four species in the eastern United States. *J Mammal* 90:743–751
- Burger RL, Van der Merwe MJ (1990) Maize and the origin of highland Chavin civilization: an isotopic perspective. *Am Anthropol* 92:85–95
- Cerling TE, Wittemyer G, Rasmussen HB, Vollrath F, Cerling CE, Robinson TJ, Douglas-Hamilton I (2006) Stable isotopes in elephant hair documents migration patterns and diet changes. *Proc Nat Acad Sci U S A* 103:371–373
- Cerling TE, Ayliffe LK, Dearing MD, Ehleringer JR, Passey BH, Podlesak DW, Torregrossa A-M, West AG (2007) Determining biological tissue turnover using stable isotopes: the reaction progress variable. *Oecologia* 151:175–189
- Chamberlain CP, Blum JD, Holmes RT, Feng X, Sherry TW, Graves GR (1997) The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141
- Cherel Y, Hobson KA (2007) Geographical variation in stable carbon isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Prog Ser* 329:281–287
- Cormie AB, Schawarcz HP, Gray J (1994) Relationship between the hydrogen and oxygen isotopes of deer bone and their use in the estimation of relative humidity. *Geochim Cosmochim Acta* 60:4161–4166
- Coulton DW, Clark RG, Hobson KA, Wassenaar LI, Hebert, CE (2009) Temporal sources of deuterium (δD) variability in waterfowl feathers across a prairie to boreal gradient. *Condor* 111:255–265
- Cryan PM, Bogan MA, Rye RO, Landis GP, Kester CL (2004) Stable hydrogen isotope analysis of bat hair as evidence for seasonal molt and long-distance migration. *J Mammal* 85:995–1001
- Cullen JT, Rosenthal Y, Falkowski PG (2001) The effect of anthropogenic CO_2 on the carbon isotope composition of marine phytoplankton. *Limnol Oceanog* 46:996–998
- Drucker DG, Bridault A, Hobson KA, Szuma E, Bocherens H (2008) Can carbon-13 in large herbivores track forest environments in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. *Paleogeog Paleoclim Paleoecol* 266:69–82
- Ehleringer JR, Bowen GJ, Chesson LA, West AG, Podlesak DW, Cerling TE (2008) Hydrogen and oxygen isotope ratios in human hair are related to geography. *Proc Nat Acad Sci U S A* 105:2788–2793

- Ezzo J, Johnson A, Price CM, Price TD (1997) Analytical perspective on prehistoric migration: a case study from east-central Arizona. *J Archaeol Sci* 24:447–466
- Farmer A, Cade BS, Torres-Dowdall J (2008) Fundamental limits to the accuracy of deuterium isotopes for identifying spatial origins of migratory animals. *Oecologia* 158:183–192
- Faure G (1977) Principles of isotope geology, 2nd edn. Wiley, New York
- Font L, Norwell GM, Pearson DG, Ottley CJ, Willis SG (2007) Sr isotope analysis of bird feathers by TIMS: a tool to trace bird migration paths and breeding sites. *J Anal Atom Spectrom* 22:513–522
- Fouré F, Merren T, Morrison J, Wassenaar LI, Hobson KA (1998) Application of EA Pyrolysis-IRMS δD and $\delta^{18}O$ analysis to Animal Migration Patterns. Micromass UK Ltd, Application Note 300
- Fox T, Hobson KA, Kahlert J (2009) Isotopic evidence for differential protein contributions to Greylag Goose (*Anser anser*) feathers. *J Avian Biol* 40:108–112
- Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2009) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen G, Dawson T, Tu K (eds) Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping. Springer-Verlag, New York
- Graustein WC (1989) $^{87}Sr:^{86}Sr$ ratios measure the sources and flow of strontium in terrestrial ecosystems. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecology. Springer-Verlag, New York
- Graves GR, Romanek CS, Navarro AR (2002) Stable isotope signature of philopatry and dispersal in a migratory songbird. *Proc Nat Acad Sci U S A* 99:8096–8100
- Hobbs JA, Qing-zhu Y, Burton JE, Bennett WA (2005) Retrospective determination of natal habitats for an estuarine fish using otolith strontium isotope ratios. *Mar Fresh Res* 56:1–6
- Hobson KA (2003) Making migratory connections with stable isotopes. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer-Verlag, Berlin
- Hobson KA (2008) Applying isotopic methods to tracking animal movements. In: Hobson KA, Wassenaar LI (eds) Tracking animal migration using stable isotopes. Academic, London
- Hobson KA, Clark RG (1992a) Assessing avian diets using stable isotopes. II: factors influencing diet-tissue fractionation. *Condor* 94:189–197
- Hobson KA, Clark RG (1992b) Assessing avian diets using stable isotopes. I: turnover of carbon-13 in tissues. *Condor* 94:181–188
- Hobson KA, Norris DR (2008) Animal migration: a context for using new techniques and approaches. In: Hobson KA, Wassenaar LI (eds) Tracking animal migration using stable isotopes. Academic, London
- Hobson KA, Wassenaar LI (1997) Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109:142–148
- Hobson KA, Wassenaar LI (2008) Tracking animal migration using stable isotopes. Academic, London
- Hobson KA, Alisauskas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95:388–394
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- Hobson KA, Wassenaar LI, Taylor OR (1999) Stable isotopes (δD and $\delta^{13}C$) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia* 120:397–404
- Hobson KA, Wassenaar LI, Milá B, Lovette I, Dingle C, Smith TB (2003) Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. *Oecologia* 136:302–308
- Hobson KA, Van Wilgenburg S, Wassenaar LI, Hands H, Johnson W, O'Melia M, Taylor P (2006) Using stable-hydrogen isotopes to delineate origins of Sandhill Cranes harvested in the Central Flyway of North America. *Waterbirds* 29:137–147
- Hobson KA, Van Wilgenburg S, Wassenaar LI, Moore F, Farrington J (2007) Estimating origins of three species of neotropical migrants at a Gulf coast stopover site: combining stable isotope and GIS tools. *Condor* 109:256–267

- Hoppe KA, Koch PL, Carlson RW, Webb SD (1999) Tracking mammoths and mastodons: reconstruction of migratory behavior using strontium isotope ratios. *Geology* 27:439–442
- Ingram BL, Weber PK (1999) Salmon origin in California's Sacramento-San Joaquin river system as determined by otolith strontium isotopic composition. *Geology* 27:851–854
- Kelly JF, Atudorei V, Sharp ZD, Finch DM (2002) Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia* 130:216–221
- Kelly JF, Bearhop S, Bowen GJ, Hobson KA, Norris DR, Wassenaar LI, West JB, Wunder MB (2008) Future directions and challenges for using stable isotopes in advancing terrestrial animal migration research. In: Hobson KA, Wassenaar LI (eds) *Tracking animal migration using stable isotopes*. Academic, London
- Kennedy BP, Folt CL, Blum JD, Chamberlain CP (1997) Natural isotope markers in salmon. *Nature* 387:766–767
- Kennedy BP, Blum JD, Folt CL, Nislow KH (2000) Using natural strontium isotopic signatures as fish markers: methodology and application. *Can J Fish Aquat Sci* 57:2280–2292
- Kennedy BP, Klaue A, Blum JD, Folt CL, Nislow KH (2002) Reconstructing the lives of fish using Sr isotopes in otoliths. *Can J Fish Aquat Sci* 59:925–929
- Koch P, Halliday AN, Walter LM, Stearly RF, Huston TJ, Smith GR (1992) Sr isotopic composition of hydroxyapatite from recent and fossil salmon: the record of lifetime migration and diagenesis. *Earth Planet Sci Lett* 108:277–287
- Koch PL, Heisinger J, Moss C, Carlson RW, Fogel ML, Behrensmeyer AK (1995) Isotopic tracking of change in diet and habitat use in African elephants. *Science* 267:1340–1343
- Larson K, Hobson KA (2009) Assignment to breeding and wintering grounds using stable isotopes: a comment on lessons learned by Rocque et al. *J Ornithol* 150:709–712
- Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird using stable carbon isotopes. *Science* 282:1884–1886
- Marra PP, Norris DR, Haig SM, Webster MS, Royle JA (2006) Migratory connectivity. In: Crooks KR, Sanjayan MA (eds) *Connectivity conservation*. Cambridge University Press, New York
- Martinez del Rio C, Anderson-Sprecher R (2008) Beyond the reaction progress variable: the meaning and significance of isotopic incorporation data. *Oecologia* 156:765–772
- Mazerolle D, Hobson KA (2005) Estimating origins of short-distance migrant songbirds in North America: contrasting inferences from hydrogen isotope measurements of feathers, claws, and blood. *Condor* 107:280–288
- McCulloch M, Cappo M, Aumend J, Muller W (2005) Tracing the life history of individual barramundi using laser ablation MC-ICP-MS Sr-isotopic and Sr:Ba ratios in otoliths. *Mar Fresh Res* 56:637–644
- McKechnie AE, Wolf BO, Martinez del Rio C (2004) Deuterium, stable isotope ratios as tracers of water resources use: an experimental test with rock doves. *Oecologia* 140:191–200
- Nadelhoffer KJ, Fry B (1994) Nitrogen isotope studies in forest ecosystems. In: Lajtha K, Michener RH (eds) *Stable isotopes in ecology and environmental science*. Blackwell Scientific, Oxford
- Pardo LH, Nadelhoffer KJ (2009) Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales. In: West JB, Bowen G, Dawson T, Tu K (eds) *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping*. Springer-Verlag, New York
- Podlesak DW, Torregrossa AM, Ehleringer JR, Dearing MD, Passey BH, Cerling TE (2008) Turnover of oxygen and hydrogen isotopes in the body water, CO₂, hair and enamel of a small mammal after a change in drinking water. *Geochim Cosmochim Acta* 72:19–35
- Popp BN, Graham BS, Olson RJ, Hannides CCS, Lott MJ, Lopez-Ibarra GA, Galvan-Magana F, Fry B (2007) Insight into the trophic ecology of Yellowfin Tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson TE, Siegwolf RTW (eds) *Stable isotopes as indicators of ecological change*. Academic, London
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* 83:703–718

- Quillfeldt P, McGill RAR, Furness RW (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Mar Ecol Prog Ser* 295:295–304
- Ramos FC, Wolff JA, Tollstrup DL (2004) Measuring $^{87}\text{Sr}:^{86}\text{Sr}$ variations in minerals and ground-mass from basalts using LA-MC-ICPMS. *Chem Geol* 211:135–158
- Reich KJ, Bjorndal KA, Bolten AB (2007) The “lost years” of green turtles: using stable isotopes to study cryptic life stages. *Biol Lett* 3:712–714
- Robbins CT, Felicetti LA, Sponheimer M (2005) The effect of dietary protein quality on nitrogen isotope discrimination in mammals and birds. *Oecologia* 144:534–540
- Rubenstein DR, Hobson KA (2004) From birds to butterflies: animal movement patterns and stable isotopes. *Trends Ecol Evol* 19:256–263
- Rubenstein DR, Chamberlain CP, Holmes RT, Ayres MP, Waldbauer JR, Graves GR, Tuross NC (2002) Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science* 295:1062–1065
- Schell DM (2001) Carbon isotope ratio variations in Bering Sea biota: the role of anthropogenic carbon dioxide. *Limnol Oceanogr* 46:999–1000
- Schell DM, Saube SM, Haubenstein N (1988) Natural isotope abundances in bowhead whale (*Balaena mysticetus*) baleen: markers of aging and habitat usage. In: Rundel PW, Ehleringer JR, Nagy KA (eds) *Stable isotopes in ecological research*. Springer Verlag, New York
- Schell DM, Barnett BA, Vinette K (1998) Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort Seas. *Mar Ecol Prog Ser* 162:11–23
- Sheppard SMF, Neilsen RL, Taylor HP (1969) Oxygen and hydrogen isotope ratios of clay minerals from porphyry copper deposits. *Econ Geol* 64:755–777
- Sponheimer M, Robinson TF, Cerling TE, Tegland L, Roeder BL, Ayliffe L, Dearing MD, Ehleringer JR (2006) Turnover of stable carbon isotopes in the muscle, liver, and breath CO_2 of alpacas (*Lama pacos*). *Rapid Commun Mass Spectrom* 20:1395–1399
- Szép T, Møller AP, Vallner J, Kovacs B, Norman D (2003) Use of trace elements in feathers of sand martin *Riparia riparia* for identifying moulting areas. *J Avian Biol* 34:307–320
- Taylor HP Jr (1974) An application of oxygen and hydrogen isotope studies to problems of hydrothermal alteration and ore deposition. *Econom Geol* 69:843–883
- Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta analysis. *Oecologia* 136:169–182
- Vogel JC, Eglinton B, Auret JM (1990) Isotope fingerprints in elephant bone and ivory. *Nature* 346:747–749
- Walther BD, Thorrold SR (2006) Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. *Mar Ecol Prog Ser* 311:125–130
- Walther BD, Thorrold SR (2008) Geochemical signatures in otoliths record natal origins in American shad. *Trans Am Fish Soc* 137:57–69
- Wassenaar LI (2008) An introduction to light stable isotopes for use in terrestrial animal migration studies. In: Hobson KA, Wassenaar LI (eds) *tracking animal migration with stable isotopes*. Academic, New York
- Wassenaar LI, Hobson KA (2000) Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. *Ecol Appl* 10:911–916
- Wassenaar LI, Hobson KA (2001a) A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Env Sci Technol* 35:1845–1850
- Wassenaar LI, Hobson KA (2001b) Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes Environ Health Stud* 39:1–7
- Wassenaar LI, Hobson KA (2006) Stable-hydrogen isotope heterogeneity in keratinous materials: mass spectrometry and migratory wildlife tissue sampling strategies. *Rapid Comm Mass Spectrom* 20:1–6
- Weber PK (2002) Geochemical markers in the otoliths of Chinook salmon in the Sacramento-San Joaquin river system, California. Ph.D. Dissertation, University of California, Berkeley, CA

- West JB, Bowen GJ, Cerling TE, Ehleringer JR (2006) Stable isotopes as one of nature's ecological recorders. *Trends Ecol Evol* 21:408–414
- Wolf B, Martinez del Rio C (2000) Use of saguaro fruit by white-winged doves: isotopic evidence of a tight ecological association. *Oecologia* 124:536–543
- Woodhead J, Swearer S, Hergt J, Maas R (2005) In situ Sr-isotope analysis of carbonates by LA-MC-ICP-MS: interference corrections, high spatial resolution and an example from otolith studies. *J Anal At Spectrom* 20:22–27
- Wunder MB, Norris DR (2008) Improved estimates of certainty in stable-isotope based methods for tracking migratory animals. *Ecol Appl* 18:549–559
- Yapp CJ, Epstein S (1982) Climatic significance of the hydrogen isotope ratios in tree ring cellulose. *Nature* 297:636–639
- Zazzo A, Harrison SM, Bahar B, Moloney AP, Monaghan FJ, Scrimgeour CM, Schmidt O (2007) Experimental determination of dietary carbon turnover in bovine hair and hoof. *Can J Zool* 85:1239–1248