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C. Stable Isotopes and Trace Elements

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INTRODUCTION

Raptors are relatively large migratory birds and as such are amenable to being equipped with both radio and satellite transmitters. Radio and satellite tracking provide the very best information on individual movements and making connections between breeding, wintering, and stopover sites (Webster et al. 2001). However, in addition to expense and limitations of battery life, like all mark-and-recapture techniques where "recapture" is a locational fix, tracking is limited by the initial marked sample, which is not necessarily representative of the population of interest. This also applies to the use of leg bands and other external markers. Such concerns can be overcome to some degree by the use of endogenous markers, which, because initial marking is not required, rely only on the recaptured population (Rubsenstein and Hobson 2004). Endogenous markers of interest include naturally occurring stable-isotope and trace-element profiles as well as genetic and other molecular markers. Here, I focus on the use of stable isotopes and trace elements to track spatial movements of raptors. Interestingly, raptors have figured prominently in the development of these techniques.

STABLE ISOTOPES

Isotopes are forms of an element that differ only in atomic mass due to a differential number of neutrons in the nucleus. Typically, they have identical chemical properties, but their mass difference confers different kinetic properties on molecules that include them. Stable-isotope abundance of any element is usually expressed as a ratio of the more rare, heavy form to that of the more common, lighter form. Stable-isotope ratios of light elements of greatest interest to ecological applications are those of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), sulfur ($^{34}S/^{32}S$), hydrogen ($^{2}H/^{1}H$) and oxygen ($^{18}O/^{16}O$). Isotopes of heavier elements such as strontium (^{87}Sr) and lead (^{210}Pb) also are particularly useful but require more involved analytical procedures. Stable-isotope ratios of the light elements are measured with isotope-ratio mass spectrometry (IRMS) and are expressed in abundance relative to international standards in delta (δ) notation, and are reported as parts-per-thousand deviation from those standards. This is an extremely well-established field in analytical chemistry and highly accurate measurements are routinely achieved in most laboratories. Fortunately, various biogeochemical processes in nature result in materials that differ in their stable-isotope abundance and these differences can be exploited to infer origins of organisms that come into equilibrium with local food webs.

The basic premise of all stable-isotope applications to animal studies is that isotopic abundance in diet is related directly to isotopic abundance in the consumer. In many cases, consumer tissues differ in their isotopic composition relative to diet by a relatively constant discrimination factor. This simple relationship brings up two important principles in applying stable isotope measurements to food webs in general and to migratory tracking in particular. First, the diet-tissue isotopic discrimination factor can be tissue-specific and these specifications may need to be established experimentally

(Hobson and Clark 1992a). Second, for metabolically active tissues, this relationship is not static but is based on equilibrium time constants related to elemental turnover rates in the tissue (Hobson and Clark 1992b). Thus, choice of tissue is of fundamental importance when deciphering isotopic information. For example, Duxbury et al. (2003) provided experimental evidence that juvenal down or juvenal plumage, but not natal down, of nestling Peregrine Falcons (*Falco peregrinus*) accurately reflects their local diet. Three key components must be considered when inferring origins of migrant birds: (1) the isotopic signature of the source and how this varies spatially, temporally, or both, (2) the isotopic discrimination associated with the tissue being used to reflect that source, and (3) the isotopic turnover rate of that tissue.

CHOICE OF TISSUE

Tissues for isotopic measurement can be metabolically active or inactive. Metabolically active tissues provide a "moving window" of past origins and the width of that window depends on the elemental turnover rate associated with that tissue. For fast-metabolic-rate tissues like liver or blood plasma, the window is in the order of a week (Hobson and Clark 1992a). Muscle and whole blood have slower turnover rates and information can be derived for a period of the order of up to six weeks. Bone collagen has an exceptionally slow turnover rate and so can provide dietary information averaged over years. The problem facing researchers who wish to use metabolically active tissues to infer origins of migratory birds is that precise metabolic turnover rates for wild, migrating birds essentially are unknown (Hobson 2005a).

Metabolically inactive tissues including keratin of feathers and talons present information on origins typical of the period of growth (assuming no endogenous reserves are used in their formation). In cases involving raptors whose molt schedules are well known, the isotopic measurement of a single feather can be a powerful tool in determining migratory connectivity. The disadvantage to using feathers is that if they are lost they can be replaced at locations other than those where they first grew. In addition, we still do not understand molt schedules of several species well enough, and it is possible, although difficult to corroborate, that failed breeders might leave the breeding grounds early and molt en route. The good news is that stable-isotope methods can be used to determine molt patterns as well as breeding origins. Wassenaar and Hobson (2001) confirmed that adult Swainson's Thrushes (*Catharus ustulatus*) molted flight feathers south of their actual breeding grounds. Talons of birds arriving in the spring may give good isotopic information on environments occupied on the wintering grounds because they grow relatively slowly (Bearhop et al. 2003, Mazerolle and Hobson 2005) and so will represent diet on the order of the previous weeks to months.

ISOTOPIC LANDSCAPES

Fortunately, several isotopic patterns known in nature can be exploited to infer origins of migratory birds and other organisms. These patterns vary according to individual isotopes, and how they behave in various biogeochemical reactions. For our purposes, these patterns can be grouped into dietary signals that are related to local biome or climatic conditions and "isoscapes," or to those related to larger-scale isotopic patterns based on underlying geology or continental patterns in precipitation.

The most studied and well known stable isotopic pattern in nature is that of stable carbon isotope signatures associated with photosynthetic pathways. This process is based on fundamentally different molecular fixation of carbon during photosynthesis that results either in a three- (C-3) or four- (C-4) carbon molecular substrate and corresponding different behavior of ^{13}C and ^{12}C in each case. Plants with a C-3 photosynthetic pathway have tissues that are more depleted, or lower in their $\delta^{13}C$ values, than those with a C-4 or CAM pathway. C-3 plants also show remarkable variation in $\delta^{13}C$ signature based on mechanisms associated with water-use efficiency (reviewed by Lajtha and Marshall 1994). The net result is that C-3 plants generally become more enriched in ^{13}C under more xeric conditions than under cooler or more mesic conditions (e.g., Marra et al. 1998). Hobson and Wassenaar (2001) demonstrated that wintering Loggerhead Shrikes (*Lanius ludovicianus*) in the southern United States and northern Mexico originated from areas with food webs ranging from pure C-3 to pure C-4 photosynthetic composition. However, because we do not have useful spatial resolution of the distribution of C-3 versus C-4 biomes throughout much of the range for most species, such information will be quite limited in inferring origins of birds such as shrikes (but see Still et al. 2003). CAM plants are relatively rare in North America but are well represented in dry areas by cacti. Wolf and Martinez del Rio (2000) and Wolf et al. (2002) have examined the dependence of White-winged Doves (*Zenaida asiatica*) and Mourning Doves (*Z. macroura*) on saguaro cactus (*Carnegiea gigantea*) and are currently using this as a marker for populations of doves originating in the American Southwest.

The stable isotopes of several elements including C, N, H, O, S, differ in marine versus terrestrial and freshwater food webs due to isotopic differences in inorganic nutrients available to primary production and, as a result, marine inputs to raptor diets can be traced isotopically. Lott and Smith (2006) were able to correct deuterium isotope (δD) values of feathers from nine different raptor species (see below) to account for links with marine food webs using δ^{34}S measurements. Certainly, dietary reconstructions based on raptor ingestion of seabirds or marine fish, or scavenging on marine-mammal carcasses should be relatively routine using the isotope approach, although there are cases where some terrestrial food webs overlap isotopically with marine food webs (e.g., terrestrial evaporative deposits can have similar δ^{34}S values as marine systems).

Stable-nitrogen isotope ratios (δ^{15}N) are extremely useful as indicators of trophic position (Kelly 2000). However, within terrestrial systems, land-use practices can influence stable-isotope abundance in food webs. Most notably, agricultural practices can alter δ^{15}N values in both upland and wetland systems. Soil nitrogen can vary isotopically within and among sites, but two processes can result in agricultural soils being more enriched in ^{15}N than temperate forest soils. These are the presence of animal-based fertilizers and the greater volatilization of isotopically lighter nitrogenous compounds such as ammonia from agricultural soils as a result of tillage and their lower acidity (Nadelhoffer and Fry 1994).

Deuterium

Without question, the single isotope that has shown the greatest potential for helping to elucidate origins of migratory birds in North America is deuterium. Its usefulness is based on the fact that stable-hydrogen isotope ratios in precipitation show a continent-wide pattern with a general gradient from enriched values in the southeast to more depleted values in the northwest (Fig. 1). This phenomenon is due to the fact that evaporation and precipitation are processes that can discriminate against or favor heavier, deuterium-containing water molecules and are, in turn, influenced by temperature, relative humidity, distance from oceans and elevation (see Bowen et al. 2005). Following the first avian applications by Chamberlain et al. (1997) and Hobson and Wassenaar (1997), several studies have confirmed the strong association between growing-season average δD values in precipitation and those in feathers of birds grown at those locations (Bowen et al. 2005). Meehan et al. (2001) conducted the first deuterium study on raptors using feathers of Cooper's Hawk (*Accipiter cooperii*) and confirmed the continent-wide pattern could be used to estimate natal origins of birds migrating through Florida. The growing-season deuterium precipitation map was recently constructed for Europe (Hobson 2003). Duxbury (2004) conducted an isotopic baseline study on feathers of Burrowing Owls (*Athene cunicularia*) and Peregrine Falcons with the intent of ultimately tracking migrants to natal or molt origin. However, the most comprehensive feather deuterium map for North American raptors was constructed by Lott and Smith (2006). These authors measured feather δD values from museum specimens of raptors originating from sites across North America and provide a convenient digital isotopic surface amenable to geographic information systems (GIS) queries.

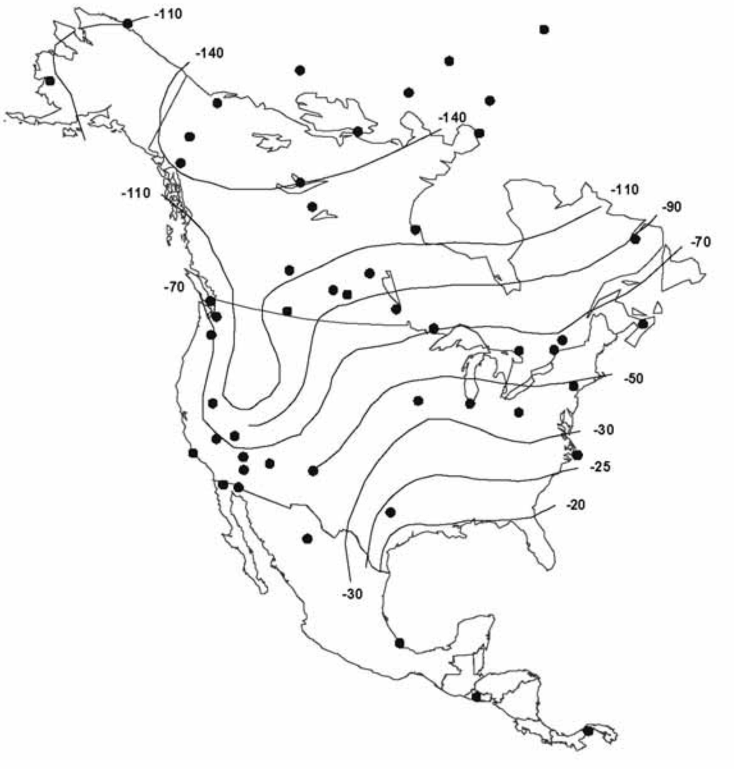

Figure 1. Pattern of growing-season average deuterium (‰) in rainfall for North America (after Hobson and Wassenaar 1997). Dots indicate long-term sampling stations. Note that feathers will be depleted relative to these contours due to isotopic discrimination.

A common question arising from the application of growing-season average precipitation contour maps for deuterium, based on the International Atomic Energy Agency (IAEA) database, is the robustness of the kriged (i.e., geographic) relationships. In any given year, how much variation in these patterns might be expected? This is not an easy question to answer because the geographical and temporal coverage in sampling sites for this database are variable. The patterns depicted by Hobson and Wassenaar (1997) and Hobson (2003) are based on about a 35-year IAEA record. However, several considerations increase our confidence in these relationships, at least qualitatively. The first is that short-term variation in precipitation signals will, to some extent, be smoothed out by the longer-term averaging of the growing season itself. Thus, in many areas, each feather measurement will, in effect, represent the average of many rainfall events and so will tend to smooth short-term fluctuations. This will not necessarily be the case in areas or times of lower precipitation or in areas that are subject to single or synoptic rainfall events. Nor will it apply to areas where groundwater or reservoirs form a significant source of hydrogen for local food webs. For a group of European sites where long-term data are available, several showed extremely small inter-year variation in average growing-season δD in precipitation, of the order of measurement error, whereas others, notably coastal sites, showed variation at least three to four times as high (Hobson 2005b). However, despite numerous potential sources of error, it is remarkable how well long-term average values of δD in precipitation are correlated with δD values of feathers grown in any given year, a relationship now demonstrated independently by several research groups. How well this relationship holds in future given climate change scenarios, of course, is unknown and will be an important area of additional research (Hobson 2005a).

Alternatives to using the long-term average contour maps include the direct measurement of isotopic patterns of interest for a particular year of interest (e.g., Hobson et al. 1999), and the creation of feather isotopic basemaps for each species or taxonomic group of interest (Duxbury 2004, Lott and Smith 2006). Meehan et al. (2003) determined that feathers grown by nestling Cooper's Hawks were more depleted in deuterium than those of attending adults grown at the same site. There are a number of possible explanations for this result including the possibility of dietary differences between age groups. Another possibility is that adult breeding raptors become relatively enriched in deuterium due to evaporative cooling throughout the extended nestling period (Meehan et al. 2003). Experiments with captive birds are needed to confirm if special consideration needs to be given to raptors when associating tissue δD values to origin.

Recently, Smith and Dufty (2005) examined feather δD values of adult and nestling Northern Goshawk (*A. gentilis*) feathers representing breeding territories across western North America. As expected, these authors found a general depletion in feather isotope δD values with latitude and distance from the coast. As with Meehan et al. (2003), these authors found that nestlings had lower δD values than adults at the same location. After controlling for location and local temperature, they also found considerable inter-individual variation in feather isotope profiles related to sex. Adult females had considerably higher δD values than males. Support was found for the hypothesis that such patterns arise from differences in evaporative cooling in those raptors that "work" during feather growth while provisioning young. These authors recommend that future studies using feathers to delineate origin should consider different isotopic basemaps for adults and juveniles.

Trace Elements

Patterns of trace elements in feathers ultimately are derived from diet, which, in turn, is influenced strongly by surficial geology, and as such are expected to provide spatial information. The use of trace elements was a comparatively early approach to using endogenous signatures in avian-migration tracking (early reviews by Means and Peterle 1982, Kelsall 1984). The method has great intuitive appeal because it is possible to measure relative abundance of numerous elements in feathers and so the chances of acquiring a unique signature for an individual or population are increased. Recent developments in analytical techniques allow the routine measurement of concentrations in feathers of numerous elements, including As, Cd, Mg, Mn, Mo, Se, Sr, Co, Fe, Zn, Li, P, Ti, V, Ag, Cr, Ba, Hg, Pb, S, Ni, and Cu. Despite the potential of this technique, the field was largely abandoned a decade ago owing to several concerns over its reliability. Some of these criticisms have since been addressed through improvement in sample-preparation and measurement techniques that made elemental measurements much more reliable, but the stigma remains.

The first attempts to use trace-element analysis to infer geographical origin were in waterfowl (e.g., Devine and Peterle 1968, Kelsall and Calaprice 1972, Kelsall et al. 1975, Hanson and Jones 1976, Kelsall and Burton 1979). These studies met with variable success but were followed by an excellent study by Parrish et al. (1983), which clearly distinguished three natal populations of Peregrine Falcons by measuring as few as five trace elements in feathers (Fig. 2; see also Barlow and Bortolotti 1988). However, several studies presented evidence of considerable intrapopulation variation in feather elemental profiles related to age (Hanson and Jones 1976) and sex (Hanson and Jones 1974, Kelsall and Burton 1979, Bortolotti and Barlow 1988). The causes of such differences are poorly understood but are likely related to hormonal and metabolic mechanisms influencing secretion of trace elements into feathers. Such variation has been problematic because it usually makes discrimination among populations difficult or may create results that are artifacts of sampling biases (Bortolotti et al. 1990).

In addition to doubts raised over intrapopulational variation in elemental profiles, a more fundamental issue that has not been addressed adequately is how such profiles change among disparate populations. For example, Bortolotti et al. (1989) found that Spruce Grouse (*Falcipennis canadensis*) from similar forest types hundreds of kilometers apart had similar feather elemental compositions, whereas those from adjacent populations occupying different forest types were quite different. Similarly, Szép et al. (2003) determined that feathers from populations of Sand Martins (*Riparia riparia*) grown at locations across Europe varied with age within colonies, and they also showed that similarity and differences in elemental profiles were not related to distance separating colonies. The value of trace-element profiles in making connections between breeding, wintering, and stopover sites, therefore, will depend on the case in question and on how spatially discrete the populations of interest are.

For highly colonial or aggregated species, it may well be possible to characterize the different colonies or breeding regions according to trace-element composition in feathers. If we are fortunate, such areas may have useful elemental fingerprints. For more dispersed species it simply may simply be impossible to describe the trace element profile patterns across the range well enough to reach unambiguous conclusions about origins. This is not to suggest that this field of research will not prove fruitful. Rather, in contrast to the use of continental deuterium precipitation maps, it will simply be difficult to make *a priori* predictions about expected trace element profiles, especially at regional scales, without detailed geological information. Trace element profiles in bird feathers may well be useful for less traditional applications. Szép et al. (2003), for example, suggested that because trace element analysis is sensitive to micro-geographical differences among individuals, this approach might be better suited to elucidating migration or wintering behavior at the level of the individual or small group. Bortolotti et al. (1990) suggested that if the effects of age and sex on trace-element profiles were well known, then population demographic information might be gleaned from elemental patterns within study populations.

Measurement techniques for establishing trace-element profiles in tissues have advanced tremendously over the last several decades. Some approaches such as Inductively Coupled Plasma (ICP) techniques require the dissolution of the sample to a liquid form prior to spectral analysis, whereas others such as the Neutron Activation Technique require that the sample be irradiated but not destroyed. Both approaches have advantages and disadvantages. The recent development of ICP-MS technology, which interfaces a mass spectrom-

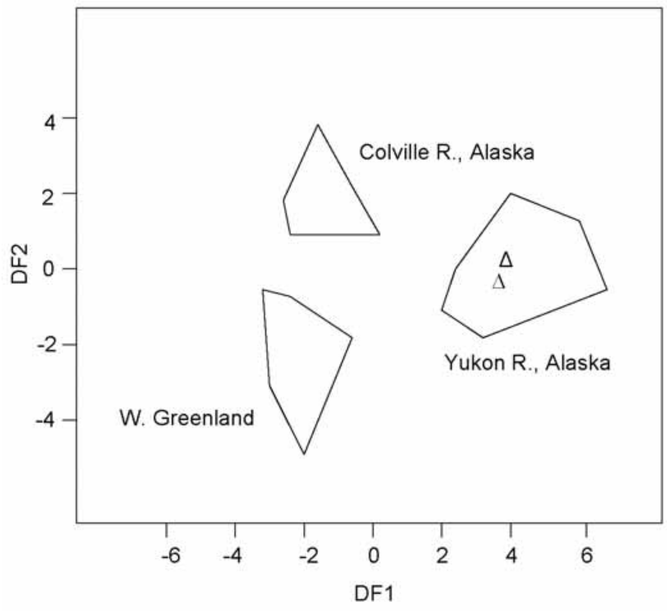

Figure 2. Trace element segregation of three populations of Peregrine Falcons (*Falco peregrinus*). Discriminant function scores based on 14 nestling feather trace-element concentrations as predictors. Polygons represent total outer boundaries of each nestling sample and Δ represents two adult birds captured at South Padre Island, Texas (after Parrish et al. 1983).

eter with an ICP machine to provide isotopic measurements of a suite of elements, certainly holds great promise for migration-tracking studies. By increasing the number of elements and species of isotopes that can be examined, it presumably allows for much greater resolution and for tracing isotope signatures hitherto impossible by more conventional MS techniques.

FUTURE DIRECTIONS

The use of stable isotopes and trace elements to track diet and geographical origins of raptors in North America and elsewhere shows significant promise and several programs are now underway that routinely collect feathers for this purpose. Clearly, an understanding of precise molt patterns for various feather tracks will be invaluable for all species of interest. Ideally, obtaining feathers that represent breeding and wintering grounds would allow analysis of two temporal and spatial samples from the same individual. Raptors can be raised in captivity and the continued investigation of isotopic and trace element behavior in experimental birds is highly encouraged.

A number of important areas require continued research (Hobson 2005a, Smith and Dufty 2005, Lott and Smith 2006). For raptors we need to know if feather growth during breeding results in increases in feather δD values and if so, how we might produce appropriate isotopic basemaps for these birds (Lott and Smith 2006). Second, we must better understand factors contributing to variance in precipitation and feather δD values and incorporate a more rigorous statistical approach to how we assign individual birds to origins. Certainly, the advent of GIS tools and Bayesian statistical techniques will be incorporated increasingly into isotopic studies involving raptors (e.g. Mazerolle et al. 2005, Wunder et al. 2005, Lott and Smith 2006). Raptor biologists and enthusiasts are uniquely positioned as a group to assist in the necessary controlled studies involving birds raised on known, isotopically homogenous diets and water sources to answer some fundamental questions related to isotope and trace element techniques. Apart from issues surrounding the evaporative cooling enrichment of raptor tissues during work, more basic information related to elemental turnover and patterns of isotopic distributions among feathers and other tissues within and between individuals are now needed.

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