Using endogenous and exogenous markers in bird conservation

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Summary

Understanding how avian populations are structured spatially and temporally is fundamental to their effective conservation. Protecting migratory species in one jurisdiction or period of the annual cycle may be ineffective if they periodically move to areas where they are not protected or are exposed to factors that limit populations or cause their decline. Unfortunately, for most species, our understanding of connectivity between breeding, wintering or stopover sites during the annual cycle are poorly understood and there is an urgent need to define such connections in order to achieve more effective conservation. This paper provides an overview of the methods used to mark individuals in order to track their movements. Passive exogenous markers such as numbered rings or bands are typically ineffective for most avian species. Active exogenous markers such as satellite tags have provided significant breakthroughs but are still prohibitive financially and still cannot be applied to species under 200g. Endogenous markers such as DNA markers, trace elements and stable isotopes show significant promise as a means of moving forward the field of animal tracking. The advantage of these endogenous approaches is that they depend only on sampling a population once and so are not biased by limitations of mark-recapture methods. Nonetheless, all methods have disadvantages and the path ahead must consider multiple approaches to tracking avian populations.

Introduction

Markers are an essential tool in wildlife conservation, both for delineating movement of individuals and, more typically, for understanding general patterns of movements of populations. The effective conservation of populations that move over large distances presents considerable challenges (Webster *et al.* 2002, Marra *et al.* 2006). For example, populations of animals might be well protected and managed at one location, but then suffer no protection once they leave that area. Long-distance migrants often encounter several geopolitical jurisdictions where conservation measures are absent or inadequate. It makes little sense to expect migratory populations to respond positively to local conservation measures if key aspects of individual fitness or overall population health are determined at another location.

The problem of conserving species that cross geopolitical borders has become a profound issue in the 21st century as habitats everywhere are being reduced in size or quality, and migrants are forced to move among a myriad of patches, each with its own level of quality, safety, and prospects for future existence (Moore *et al.* 2005, Robinson *et al.* 1995). For some animals, populations breeding in one area may follow similar migration routes and winter in the same general wintering region. In this case, we would consider the subpopulations to show *strong connectivity*. Other breeding populations may be dispersed across multiple sites often breeding with other populations of the same species that winter in different sites and so be considered a case of *weak connectivity*.

The concept of migratory connectivity is important to conservation and many forms of connectivity are possible (Webster and Marra 2005, Boulet and Norris 2006). Weak connectivity may involve individuals from many breeding populations mixing among many wintering populations or vice versa. Quantifying patterns of connectivity can be difficult. One approach is to compare observed patterns of connectivity against the null hypothesis of complete mixing based on relative abundance (Norris *et al.* 2006). The problem with this approach is that estimates of relative abundance are rarely available throughout a species entire range and populations may move in ways that do not reflect expectations based on simple overall patterns of abundance.

Populations with strong connectivity may be most vulnerable to declines since they have little chance to be 'rescued' by peripherally connected populations (Marra *et al.* 2006). On the other hand, it is the strongly connected populations that may benefit the most from conservation efforts because the connections between two or more areas are well established. While populations of weakly connected individuals may be inherently 'safer', these populations will understandably be harder to manage unless measures are enacted over large regions. It may also be more difficult to identify the causes of population declines in subpopulations that are weakly connected (Marra *et al.* 2006).

Knowledge of migratory connectivity is also important to predict how conservation measures in one season influence populations the following season (Martin *et al.* 2007). Criteria for deciding where and when to conserve non-breeding habitat usually does not consider where individuals were spending the remainder of the annual cycle. So, consideration of how populations are connected can result in radically different decisions on how to allocate resources for conserving species (Wunder and Norris 2008).

Effective management of species also requires identifying where populations are most productive. Where within the often vast area that makes up a species' range are the most young being produced and recruited into the autumn migratory population and where are individuals experiencing the highest survival rates during the non-breeding period? Understanding where hotspots of productivity and survivorship occur helps us protect those places and better understand factors that may be limiting populations.

It has been recognized for some time that events occurring outside the breeding area can profoundly affect the fitness of migratory individuals (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Raveling and Heitmeyer 1989). More recently, much interest has been generated from the work of Marra *et al.* (1998) who, using stable isotopes, first demonstrated in American Redstarts *Setophaga ruticilla* a clear link between spring arrival times of males and the quality of the habitat they occupied in winter. The quality of a habitat where an animal winters will determine the level and speed with which the necessary body condition for migration can be reached, and so can determine when and in what condition that individual arrives on the breeding grounds. Several studies of birds have shown that earlier arriving birds can obtain better territories, initiate clutches sooner, and generally fledge more young than those arriving later (e.g. Gill *et al.* 2001, Bêty *et al.* 2003, Norris *et al.* 2004).

Establishing details of migratory movements and population connectivity in animals is fundamental to understanding key aspects of their evolution, life history and conservation. The field has witnessed a renaissance in recent years primarily because the development of new analytical techniques has provided some true breakthroughs. There is also a more urgent sense that we need to more quickly understand key migratory linkages for animal populations in order to help conserve them in a rapidly changing world. This paper provides a brief overview of the use of extrinsic and intrinsic markers in bird conservation with an emphasis on the use of stable isotope techniques. A more detailed coverage is provided in Hobson and Wassenaar (2008).

Extrinsic markers

Tracking migratory birds has involved numerous techniques over the years. Until very recently, all approaches involved the use of extrinsic markers applied to individuals with the hope of

relocating that same individual elsewhere, or on the use of recognized phenotypic or morphological traits that showed known geographic variation. For birds, there is a rich literature on geographic variation in plumage and morphology and these traits have been used to describe migratory connectivity. Birds captured during migration can occasionally be placed into sub populations without the need for mark-recapture techniques (Ramos and Warner 1980, Ramos 1983). However, typically the geographic resolution provided by this approach is both poor and highly variable among taxonomic groups.

By far the most widespread approach to tracking migrant birds is through the application of passive extrinsic markers. These have overwhelmingly involved leg bands or rings carrying a unique number combination and some instruction on where to report the band if it is recovered. Other markers such as coloured leg bands, patagial tags, numbered neck collars, streamers or colour dyes have also been used. Millions of individual birds have been individually tagged over the last 100 years. For a number of species with small global populations and restricted ranges, some very impressive recovery rates have been achieved (e.g. Owen and Black 1989) and some key insights into migratory connectivity established (Gill *et al.* 2001). Other success stories involving the use of numbered rings include the impressive British Trust for Ornithology (BTO) migration atlas summarizing a hundred years of recoveries. However, for the vast majority of species, extremely low recovery rates (i.e. < 0.01%) are the norm preventing inferences on connectivity *per se* (Hobson 2003).

Transmitters

Transmitters send out signals that can be intercepted with a suitable receiver device. If a receiver is within range of the transmitter, then the location of the bird can be inferred either by tracking down the individual or by triangulation with more than one receiver. Radiofrequency transmitters can be made small enough (0.5 g or lower) to place on small passerines and bats. However, miniaturization reduces both range and battery life so that these devices typically provide locations up to a few kilometres. Nonetheless, adventurous researchers have attempted to follow migrating birds, bats, and even dragonflies equipped with transmitters over at least portions of their flight paths (Wikelski *et al.* 2003, Cochran *et al.* 2004, Holland *et al.* 2006). Using a combination of aerial and ground tracking receivers, Wikelski *et al.* (2006) followed the southward migration of dragonflies equipped with 300 mg radio transmitters. Cell phone technology has also provided new possibilities for tracking animals but the miniaturization and development required for small animal tracking remains a problem (Stokely 2005). A final concern is that the fastening of markers or transmitters may alter flight or movement behaviour.

Radar technology has made great contributions to our understanding of migration since this provides information of flying animal movements over considerable distance (Gauthreaux and Belser 2003). However, like automated receivers, radar installations are often fixed, and mobile radar systems are generally impractical to follow animal movements over migratory distances. Cross-band transponders placed on migratory organisms can be used to elicit a detectable radio frequency signal after the transponder is intercepted by radar. Such *active* radar systems face a number of limitations, again related to size and weight of instrumentation and the need to intercept the organism of interest within range of the radar system (see www.earthspan.org).

Satellite transmitters have provided a major advance in methods to track migratory birds since they provide extremely accurate positions of individuals remotely. Satellite tracking systems such as ARGOS (www.argosinc.com) have been placed on different satellites from the US National Oceanic and Atmospheric Administration, The Japanese Space Agency and the European Meteorological Satellite Organization. The ARGOS system collects data from Platform Terminal Transmitters (PTTs) and delivers telemetry data back to the user. Unlike other extrinsic techniques, this approach does not require the physical capture of individuals once they are marked. Future prospects for this technology are encouraging and there is strong interest in diminishing the size of transmitters and batteries so that smaller species can be

monitored. Currently, the smallest satellite tags available are about 9.5 g and potentially could be used on 240 g animals (using the $< 5\%$ body weight rule, Murray and Fuller 2000). Unfortunately, this still excludes about 81% of the world's birds (Wikelski *et al.* 2007). In addition, there is evidence that some individuals carrying these transmitters via harness attachment may be affected in ways that alter their behaviour (Phillips *et al.* 2003).

The use of satellites may potentially provide a major breakthrough in tracking migratory animals down to the size of large insects. Wikelski *et al.* (2007) have proposed that a new satellite equipped with radio receivers could track radio-tags with radiated power as low as 1 mW with an accuracy of a few kilometres under favourable conditions. This power can be achieved from existing radio frequency tags as small as < 1 g. A group known as ICARUS (International Cooperation for Animal Research Using Space (www.icarusinitiative.org/solutions) is promoting this idea as a means of tracking small animals around the globe.

A relatively new application for tracking migratory animals is the use of archival geolocation tags (Shaffer *et al.* 2005, 2006). These tags provide data that can be used to estimate longitude and latitude based on light levels and sea-surface temperatures and long-distance movement data have now been reported on shearwaters (Shaffer *et al.* 2005) and albatross (Shaffer *et al.* 2006) with several more species currently being tested. The advantage of these tags is that they are significantly lighter than satellite transmitters (now 1.5–3 g). However, the disadvantage is that their accuracy, using both combined light levels and sea-surface temperatures, is only $\pm$ 200 km which restricts application to questions pertaining only to large-scale movements.

With the exception of satellite transmitters, all extrinsic markers require that the individual be recaptured, resighted, or at least move within detection distance at a later time. The probability of this occurring can be vanishingly small. Passive extrinsic markers suffer from another fundamental flaw – they provide information only on the movement of marked individuals. The possibility of extrapolating the findings based on a small marked cohort to the population or species levels depends on how representative the marked individuals are. A single band recovery or satellite track, while interesting and ultimately useful, may tell us very little about what populations are doing.

Intrinsic markers

The primary advantage of intrinsic markers is that initial marking of individuals is not necessary and that every capture provides information on origin. In this sense, every capture becomes a recapture. The sampling scheme is biased then, only by the limitations of where animals are ultimately located and this typically represents a much less serious form of bias compared to where individuals can be marked initially using extrinsic markers. Three types of intrinsic markers are considered here: trace elements, DNA and stable isotopes. Other markers include contaminant loads, pathogens and parasites but these have generally not been well developed to date (Hobson and Norris 2008).

Trace Elements

Relative abundance of trace elements in bird tissues is ultimately acquired through the soils and geological substrates supporting local foodwebs where tissues are formed or maintained. The principle with trace elements is that individuals acquire distinctive chemical profiles at one geographic location and then carry that profile with them to another area where they can be sampled to estimate their previous geographic origin. In the past, one of the limitations of using trace elements was the amount of sample required for analysis. However, the advent of Inductively Coupled Plasma Mass Spectrometers (ICP-MS) have allowed smaller quantities of samples (3 mg; Donavan *et al.* 2006, Norris *et al.* 2007) to be measured with relatively high precision. This technological advance has allowed researchers to focus on non-destructive tissues, such as metabolically inactive keratin (in feathers and claws), that are grown during specific

periods of the migratory cycle. Trace element profiles have been used to infer whether individuals sampled in the same breeding population originate from different places the previous winter (Szep *et al.* 2003).

Unfortunately, we have little idea of how trace elements vary over the landscape and so the ability of this technique to estimate the precise origin of individuals is currently limited. Norris *et al.* (2007) measured 42 trace elements in feathers of Western Sandpipers *Calidris mauri* at five different locations on their tropical wintering grounds. Feathers were grown during the winter periods and so provided a signature of known-origin. Elemental profiles successfully distinguished between birds wintering at all five locations. However, two locations were less than 3 km apart suggesting that trace elements are likely very specific to the location or origin in which they were sampled. In this case, estuarine regions will be influenced considerably by the trace element loads transported by local rivers. Trace element approaches are probably best suited to species that are aggregated over only a few breeding or wintering sites so the majority of populations can be sampled over the entire range (Donavan *et al.* 2006). Studies several years ago also showed that some trace elements in feathers may be acquired after growth (Bortolotti and Barlow 1988, Bortolotti *et al.* 1988). This may be the case with aerial deposition of some heavy metals and other elements (Pb, Na, Cl, Br) that can possibly bind with feather material, implying that some trace elements may be less reliable than others for tracking long-distance movements of birds (e.g. Pain *et al.* 2005).

Genetics

The use of genetics has generated considerable interest in assigning individuals to origins because it is possible to assay and describe genetic variation across breeding populations and then to use this information to assign a probability that a given individual came from a given (known) subpopulation (Smith *et al.* 2005). The identification of population structure using genetic markers has included the use of allozymes, mitochondrial DNA sequences, and DNA fragment analyses such as microsatellites and amplified fragment length polymorphism (AFLP). These markers can yield different scales of population structure because they evolve at different rates. In North America, genetic markers have been particularly useful in differentiating between eastern and western breeding origins of wintering Neotropical migrant songbirds (Smith *et al.* 2005, Boulet *et al.* 2006) reflecting patterns of rapid demographic expansions following glaciation events on that continent. Genetic analyses also hold great potential for developing parasite markers in migrant organisms since PCR-based assays of blood parasites can now identify pathogens to species and haplotype (Ricklefs *et al.* 2005).

Stable isotopes

There are several reviews that are useful to the reader interested in applying stable isotopes in ecological studies (Kelly 2000; Martinez del Rio and Wolf 2005; Karasov and Martinez del Rio 2007; Michener and Lajtha 2007). Due to variations in the number of neutrons in the nucleus, several elements occur in more than one stable form. These stable isotopes behave the same way chemically but their mass difference confers different rates of reaction in various biogeochemical processes. Mass spectrometers are instruments that provide an extremely accurate estimate of the ratio of the heavier to lighter isotope in an unknown sample relative to an international standard and this is typically expressed in the following delta notation:

$$\delta X = (R_u/R_s - 1) \times 1000 \qquad (1)$$

where X is the stable isotope (e.g. ^{13}C, ^{15}N, ^{34}S) and R is the ratio of the heavier to lighter isotope of the appropriate element ($^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{34}S/^{32}S$) in unknown or standard. The units are parts per thousand (‰). Because the international standards are arbitrary, some isotope ratios

are positive (i.e. more enriched in the heavier isotope relative to the standard) and others are negative (i.e. more depleted in the heavier isotope relative to the standard).

Applications of stable isotope methods to tracking wildlife have increased tremendously in the past decades. This development relies on three basic isotopic principles:

1) Consumer stable isotope values reflect those of the foodweb they are in equilibrium with. Should foodwebs used by a migratory organism differ isotopically and spatially, then stable isotope values in the consumer can provide unambiguous information on previous consumer locations.

2) The time period over which this spatial information is retained will depend on the tissue chosen. For metabolically active tissues, this represents a moving window of forensic information. For metabolically inactive tissues, spatial information will be locked in indefinitely but will only reflect position for the short period of integration reflecting the growth of that tissue.

3) Mechanisms related to dietary transfer of isotopic signals to consumer tissues including isotopic discrimination, exercise, and metabolic routing are known and accounted for.

In practice, it is rare that all three principles will be satisfied or known with sufficient confidence! However, depending on the organism, much of this uncertainty can be constrained and useful inferences can be made with respect to previous provenance of individuals based on isotopic measurements of their tissues.

Isotopic discrimination

The following simple equation demonstrates the isotopic linkage between a consumer and its diet:

$$\delta C_t = \delta d + \Delta_{dt}$$

Where δC_t is the measured stable isotope value of a tissue in the consumer, δd is the stable isotope value of the diet and Δ_{dt} is the diet-tissue isotope discrimination factor. Recent research has also determined that the diet-tissue discrimination factors are influenced by the quality of the diets and so are likely not static for most wild animal populations (Robbins *et al.* 2005). Since our ability to place an organism in a particular isoscape is sensitive to our knowledge of the true discrimination factors associated with an organism or dietary regime of interest, researchers should bracket their estimates based on an honest assessment of how well they know such factors.

Nitrogen isotopes

Stable nitrogen isotopes in the tissues of consumers really represents a means of tracing protein pathways derived from diet since this element is largely absent in lipids and carbohydrates. Isotopes of this element also show the largest trophic shifts or enrichment in bird tissues and so can present a problem in studies attempting to link isotopic measurements to origins unless such $\delta^{15}N$ trophic discrimination factors are well known. Another aspect of tracing origins using $\delta^{15}N$ measurements of avian tissues is that proteins in diets are composed of a number of essential and non-essential amino acids. 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 $\delta^{15}N$ measurements in consumers will reflect the degree to which the diet meets the amino acid requirement of the consumer (Robbins *et al.* 2005). In general, poorer quality diets will likely result in greater overall diet-tissue discrimination for ^{15}N than high-quality diets. 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 $\delta^{15}N$ values. For many species with very constant diets, the bulk diet-to-tissue isotopic discrimination factors will remain fairly constant. However, omnivorous birds that switch between high protein and high carbohydrate diets present a major challenge in terms of associating tissue $\delta^{15}N$ values to region.

Knowledge of these sorts of physiological processes is necessary, then, when using tissue $\delta^{15}N$ 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 $\delta^{15}N$ 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).

Carbon isotopes

Unlike nitrogen and sulphur, carbon is present in all three dietary macromolecules (protein, fat, carbohydrates) and so $\delta^{13}C$ measurements of consumer tissues will reflect these various sources. The more varied sources of carbon to bird tissues undoubtedly contributes to more variable diet-tissue $\delta^{13}C$ discrimination factors compared to those found for most of the other light elements. However, in many cases, lipids in diets are transferred directly with little isotopic modification to lipids in the consumer. Carbohydrates are often burned directly for energy production producing CO_2 as the only carbon by-product, and hence $\delta^{13}C$ values in breath CO_2 can be used as a means of directly tracing origins of carbohydrates in diet (Podlesak *et al.* 2005). Carbon isotope values of proteins can theoretically originate from all three dietary macromolecules but is more likely to be associated with dietary proteins, especially for carnivores.

Sulphur isotopes

Sulphur in consumer tissues is derived from the sulphur-bearing amino acids (e.g. cystein, methionine) and so $\delta^{34}S$ measurements are closely linked to dietary protein pathways. Unlike the other light isotopes, we expect little S isotopic discrimination between diets and consumer tissues again due to the little opportunity for the essential amino acids to be isotopically modified in consumers. As a result, $\delta^{34}S$ measurements make for a useful direct tracer in foodweb and migration studies (Krouse *et al.* 1991, Hebert and Wassenaar 2005).

Hydrogen and oxygen isotopes

Hydrogen is a particularly useful element for tracking migratory wildlife. However, this element presents a number of challenges in terms of understanding how the δD measurements of consumer tissue relates to hydrogen sources which, in most terrestrial systems, is driven by the global water cycle driving primary production. Like carbon, hydrogen occurs in all three dietary macromolecules and so recognition of metabolic routing is important. However, the most interesting challenge is the fact that a portion of the hydrogen in any tissue exchanges with body water, a component which is presumably more labile than dietary derived hydrogen. Drinking water as well as diet thus constitutes a source of hydrogen in animals (Hobson *et al.* 1999).

The use of $\delta^{18}O$ measurements to track wildlife is in its infancy due to previous technological constraints of routinely measuring oxygen isotopes in animal tissues. That situation has now changed due to on-line pyrolytic techniques. In many systems, there is a tight coupling between $\delta^{18}O$ and δD values due to the meteoric relationship (reviewed by Wassenaar 2008). Thus, in many cases, no additional information will be derived from performing $\delta^{18}O$ measurements in addition to δD measurements on the same tissue. As well, δD values typically span a much larger range than $\delta^{18}O$ measurements in terrestrial foodwebs and so can potentially provide greater resolution with respect to source discrimination and an overall better signal to noise ratio. Oxygen occurs in proteins but not in lipids or carbohydrates. However, sources of oxygen include diet, drinking water and air and so, like hydrogen, it is difficult to predict isotopic

discrimination factors associated with each contribution and ''working values'' will need to be derived largely from future examination of wild and captive animals.

Isotopic turnover – the moving window

That stable isotope values in consumer tissues reflect an integration of feeding events over various time periods has been known and experimentally demonstrated for decades. (Tieszen *et al.* 1983). This approach has now been used by several researchers examining various species and most have fit an exponential uptake curve to describe the pattern of isotopic change in tissues following an isotopic diet shift:

$$D(t) = a + b\exp(-ct)$$

Where D(t) is the stable isotope value of the tissue at time *t*, *a* is the asymptotic tissue value, *b* is the absolute change in tissue isotope value between initial and asymptotic conditions, and *c* is a rate constant defining tissue turnover. This approach has worked well to provide estimates of elemental turnover rates in various tissues of birds, fish and mammals (e.g. Hesslein *et al.* 1993, Bosley *et al.* 2002, Dalerum and Angerbjörn 2005). However, a key assumption of this approach is that the organism of interest is in *equilibrium* with its diet. Fitting the exponential model to non-equilibrium situations can result in erroneous estimates of the half life of elements in the consumer's tissues. Recently, Cerling *et al.* (2007) have provided an alternate approach to estimating turnover rates that is particularly sensitive to consumer tissue isotope values being derived from more than one source pool. This reaction progress variable approach appears to be able to detect the expected different turnover rates associated with essential (i.e. rapid uptake from diet) and non-essential (i.e. slower uptake due to a lag effect in protein production) amino acids.

A potential disadvantage of previous studies establishing turnover rates in birds is that they were necessarily based on sedentary, non-exercised individuals in laboratory settings. Might we not expect more rapid elemental turnover in tissues of exercising vs. sedentary organisms? This is still not clear but Hobson and Yohannes (2007) used Rosy Starlings (*Sturnus roseus*) trained to fly in a wind tunnel to provide a first approximation of this effect for the cellular fraction of blood and found no difference between the two groups. Elemental turnover rates also appear to follow expectations based on allometry (Carleton and Martinez del Rio 2005). It is possible, then, to estimate turnover rates for various tissues based on the body mass of the organism of interest even though that species has not been tested experimentally.

Applications of stable isotopes to tracking bird movements

The recent development of stable isotope methods to tracking migratory wildlife has already provided a rich literature to illustrate the breadth of applications using the light isotopes of C,N,H,O,S. (reviewed in Hobson 1999a, Rubenstein and Hobson 2004, Hobson 2005a, Hobson 2008). In general, these applications can be split into 1) inferences of animal origins based on biome markers, typically using isotopes of C,N,S and 2) those using continental-scale δD isoscapes. The use of δD measurements has brought with it immense opportunities but also challenges as we attempt to fill in the information gaps associated with this complicated element and so hydrogen will be discussed separately.

Migratory movement among isoscapes

Some of the earliest isotopic investigations revealed distinct differences between marine and terrestrial foodwebs with marine organisms typically having more positive $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, δD and $\delta^{18}O$ values compared to their terrestrial counterparts (Hobson 1999a). As many migratory

birds use both terrestrial and marine biomes throughout their annual cycles, these marine versus terrestrial isotopic differences have become extremely useful (e.g. Atkinson *et al.* 2005). Currently, there is also great interest in establishing marine isoscapes that can be used to help track the movements of marine birds (Hobson 2007, Gómez-Diaz and González-Solis 2007). Plant physiologists have also pioneered the use of stable isotope measurements to discern C3, C4 and CAM-based photosynthetic pathways using both $\delta^{13}C$ and δD measurements and have more recently investigated the effect of water-use efficiency mechanisms in C3 plants which generally leads to an enrichment of plant tissue ^{13}C.

Africa is a continent that has attracted a number of isotopic studies over the years. Terrestrial foodwebs in Africa also include varied C3 and C4-dominated isoscapes and a very diverse and dynamic δD isoscape. Two simultaneous yet independent studies used stable isotope measurements of African Elephant *Loxodonta africana* ivory and bone collagen to infer origins of that material as a forensic tool to counter the illegal ivory trade (van der Merwe *et al.* 1990, Vogel *et al.* 1990). Elephants feeding primarily on grasses sample a C4 foodweb and so have more positive $\delta^{13}C$ values compared to those feeding in woodlands on C3 browse. Elephants feeding in more arid areas may also have higher $\delta^{15}N$ values than those in more mesic habitats (Heaton 1987). Combined with assays of Pb and Sr isotopes, these studies showed strong segregation among several African Elephant populations and underlined the forensic utility of stable isotopes to infer origins of several taxa. However, strong year-to-year variations in foodweb $\delta^{15}N$ values within the Amboseli National Park due to climatic variation presented a challenge (Koch *et al.* 1995). This illustrates the need to know the natural range of variation (NRV) in stable isotope patterns spatially and temporally when evaluating the accuracy of the technique when inferring animal origins.

Fortunately, many terrestrial systems are less dynamic isotopically and strong and consistent isotopic differences are maintained over decadal or longer timeframes. This is especially the case with the use of $\delta^{13}C$ measurements to track the use by animals of C3, C4 and CAM foodwebs. Hobson (1999b) showed that migrant insectivorous songbirds known to originate in boreal forest of North America had consistently lower feather $\delta^{15}N$ values than those species from more southern agricultural zones. Similarly, Hebert and Wassenaar (2001) were able to use $\delta^{15}N$ measurements to segregate waterfowl originating in agricultural zones which are typically enriched in ^{15}N compared to more natural temperate regions (see also Hobson *et al.* 2005).

A seminal study by Wolf and Martinez del Rio (2000) on the isotopic ecology of two species of doves using a desert region in the southwestern United States provides an excellent example of how tissue δD and $\delta^{13}C$ measurements can provide strong inferences on the diets, and hence feeding locations of birds. The Saguaro Cactus *Carnegiea gigantea* represents a valuable food and water resource to animals in arid environments. This CAM resource is imbedded in a C3 plant biome and so fruit consumption can be traced by $\delta^{13}C$ measurements. However, water derived from CAM plants is also highly enriched in deuterium compared with surface waters and this provided evidence that while the two species consumed food from the Saguaro, they differed in their dependence of this plant for drinking water.

Other studies have exploited the strong C4 $\delta^{13}C$ signal of agricultural corn to infer the origins of migratory herbivorous birds. Alisauskas *et al.* (1998) assigned newly arriving Lesser Snow Geese (*Chen caerulescens*) to a migratory staging area in the Missouri Valley, USA, since local birds subsisted largely on corn agriculture whereas immigrants arrived from distinct C3 habitats or non-corn growing regions to the south. In their study of feathers of Red-winged Blackbirds *Agelaius phoeniceus* across a latitudinal gradient in North America, Wassenaar and Hobson (2000) found that birds formed feathers from pure C3 to pure C4 foodwebs. Similar results were found for Loggerhead Shrikes *Lanius ludovicianus* on that continent (Hobson and Wassenaar 2001). Both of these examples indicate the way in which corn and other agricultural C4 crops imbedded in a C3 landscape can provide information on origins of migrant animals.

A study which clearly had profound influence on the field of identifying seasonal interactions or carry over effects from one season to another was that of Marra *et al.* (1998). Those authors examined the effect on tissue $\delta^{13}C$ values of American Redstarts occupying habitat of different quality on the Jamaica wintering grounds. Likely due to the effect of water-use efficiency in C3 plants, foodwebs in wet mangrove forest were more depleted in ^{13}C than those in xeric scrub habitat and such habitat markers were passed on to redstarts inhabiting those habitats. Long-term studies on this wintering population of redstarts suggested that those birds occupying the better (moister) habitat were the first to reach a body condition which allowed them to migrate back to the United States and Canada to breed. Thus, the prediction was that early spring arriving male birds in New Hampshire would have muscle tissue relatively depleted in ^{13}C compared to later arriving birds. This was indeed the pattern that was found. Bearhop *et al.* (2004) also demonstrated the utility of using stable isotope measurements of slow growing claw material in birds and intercepted Black-throated Blue Warblers *Dendroica caerulescens* during migration in the Bahamas. Similar to the Marra *et al.* (1998) study, they found that birds in better body condition were from more mesic (moist) vs. xeric (dry) habitats as shown by their claw $\delta^{13}C$ values.

Chamberlain *et al.* (2000) investigated $\delta^{13}C$ and $\delta^{15}N$ values in feathers of Willow Warblers *Phylloscopus trochilus* located along a breeding latitudinal gradient in Scandinavia. Two subspecies are segregated along this gradient that differ in morphology and assumed African wintering grounds based on a handful of band returns. Unlike most Nearctic migratory birds, several Palaearctic species replace flight feathers on their wintering ground in Africa and so it was possible to infer aspects of the wintering habitats using isotopic analyses of these feathers. Southern *trochilis* subspecies had feathers more indicative of the mesic habitats of sub-Saharan West Africa than the northern *acredula* subspecies with supposed wintering areas Central, East or South Africa. These results agreed generally with the limited band return data and with isotopic analysis of moulting birds from known capture sites in Africa (Bensch *et al.* 2006) However, the follow-up study using a larger dataset by Bensch *et al.* (2006) found higher $\delta^{13}C$ values in general than those found by Chamberlain *et al.* (2000). This discrepancy is somewhat reminiscent of the forensic analysis of African ivory and the warning by Koch *et al.* (1995) that $\delta^{13}C$ and $\delta^{15}N$ isoscapes in some regions of Africa may be highly variable among years.

Barn Swallows *Hirundo rustica* breeding in Denmark are known to winter in south Africa but more refined information on connectivity is not available. Møller and Hobson (2004) investigated δD, $\delta^{13}C$, and $\delta^{15}N$ values in African-grown feathers of Danish swallows and discovered that the distribution of $\delta^{13}C$ and $\delta^{15}N$ values was bimodal, with a rare group (6% of the population) having very different values compared to the main group. These researchers concluded that this represented different winter habitats or regions occupied in Africa by the two groups. The current hypothesis is that this rare group in Denmark originated from breeding populations within Scandinavia. The deliberate analysis of the isotopic structure of breeding populations of birds can also be used as a means of detecting immigrants into those populations. Hobson *et al.* (2004a) used this approach to investigate minimum estimates of dispersal into breeding populations of American Redstarts and Ovenbirds *Seiurus aurocapillus* using δD measurements of feathers. Isotopic tools used to identify dispersing individuals into breeding or wintering populations represents a valuable conservation tool since it can ultimately provide information on the dynamics of population movements.

Møller *et al.* (2006) continued their isotopic analysis of Barn Swallows in Europe by examining those populations occurring within and outside the zone of influence of the Chernobyl nuclear accident and for samples obtained before and after the incident. They determined that correlation between $\delta^{13}C$ and $\delta^{15}N$ values in winter-grown feathers differed significantly between regions for females but not for males. This was interpreted as indicating that birds from the non-Chernobyl region were composed of females from a smaller recruitment area. The reasoning was that individuals with greater dispersal distance moulted their feathers across a larger wintering area thus increasing the probability of higher isotopic variance. Weak

positive δ¹³C and δ¹⁵N correlations within 'isotopic populations' seem to be common and the decoupling of this relationship might be a good indicator of mixed populations.

The movement of animals between marine, estuarine and terrestrial or freshwater habitats holds great potential for inferring their past habitat use and potential migratory origins. Tietje and Teer (1988) were among the first to use stable isotope methods to investigate how wintering Northern Shoveler *Anas clypeata* use coastal and inland freshwater wetlands and were able to demonstrate sedentary behaviour among late wintering individuals. Other studies have primarily used δ¹³C measurements to infer movement of piscivorous birds between marine and freshwater habitats (Mizutani *et al.* 1990, Bearhop *et al.* 1999) and Hobson (1987) even used this approach to infer use of garbage dumps by coastal wintering gulls near an urban center.

The deuterium breakthrough

Deuterium values 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). Previous studies had also established strong correlations between growing season average δD values in precipitation and those in plant biomass (Yapp and Epstein 1982). However, it was the work of Cormie *et al.* (1994) on deer bone collagen that first clearly demonstrated that such patterns were also passed on to organisms at higher trophic levels, and 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 advantage to using birds was that their moult chronologies are relatively well known and most migrants breeding in the United States and Canada moult flight feathers prior to their southward migration. The ability to capture an individual on the wintering grounds and use its feather to predict an approximate latitude of breeding origin was indeed a major breakthrough and 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 has since been confirmed by several other researchers on various avian species (Hobson 2008).

Several recent applications using δD measurements have involved migratory birds in North America and have had a strong conservation motivation. Populations of Loggerhead Shrike have declined in North America and Hobson and Wassenaar (2001) and Perez and Hobson (2006) investigated the structure of wintering populations in the southern USA and north-central Mexico. They were able to show that both Mexico and Florida were important wintering areas for northern breeding populations of this species. Since previous few band returns over the last 50 years pointed only to Texas, this work quickly identified new areas of potential concern. Bicknell's Thrush *Catharus bicknelli* currently breeds in precariously small island habitats in the eastern United States and winters in the Caribbean. Based on a sample of birds wintering in the Dominican Republic, Hobson *et al.* (2004b) determined that a significant proportion of the population bred further north, likely in southern Quebec. A similar study using both δD and δ¹³C measurements of Black-throated Blue Warblers on the wintering grounds revealed an important split in origins with those birds breeding in the south wintering in the eastern Antilles and those breeding in the north wintering in the west (Rubenstein *et al.* 2002). That southern populations seem to be declining compared to the northern populations suggests that deforestation patterns on the wintering grounds may be a factor.

Other important advances, especially with migrant songbirds has involved the delineation of catchment areas of constant-effort migration monitoring stations for a variety of species (Wassenaar and Hobson 2001, Mazerolle *et al.* 2005, Dunn *et al.* 2006). By defining the approximate origins of birds caught during migration, analysis of population trends from these stations will be enhanced.

Another aspect of wildlife management concerns an understanding of where within the range of a species most of the young are produced. This is especially important for highly managed game species that are harvested during their fall migration and on the wintering grounds. Hobson *et al.* (2006) defined the origins of harvested Sandhill Cranes *Grus canadensis* through the central Flyway of North America using δD measurements of feathers and claws and identified the Hudson Bay lowlands and southern boreal forest as regions of highest productivity.

Other applications of the deuterium basemap for North America have been attempts to evaluate population structure and connectivity of migratory songbirds. By sampling birds across the wintering grounds, preliminary pictures are now emerging for Yellow Warbler *Dendroica petechia* (Boulet *et al.* 2006), American Redstart (Norris *et al.* 2006), Henslow's Sparrow *Ammodramus henslowii* (Ibargűen 2004), Loggerhead Shrike (A. Chabot *et al.*, unpubl. data), and Mountain Plover *Charadrius montanus* (Wunder 2007). These studies are primarily limited by the amount and geographical extent of winter captures. Kelly *et al.* (2002) also nicely demonstrated a ''leapfrog'' migration system in western populations of Wilson's Warbler *Wilsonia pusilla*.

An interesting aspect of the behaviour of δD is that deuterium in precipitation tends to rain out more at lower elevations than at higher elevations. This is a well known phenomenon and results in an altitudinal 'depletion' in δD by -1 to -4 ‰ per 100 m rise in elevation, depending on the gradient and temperature change (Clark and Fritz, 1997). Similarly, the demands of plant adaptations to harsher growing conditions at higher altitudes tends to result in plants with higher $\delta^{13}C$ values at higher elevations. Since there are several species that perform altitudinal migrations, especially in the tropics, it was of interest to see if tissues grown along an altitudinal gradient reflected such patterns. Hobson *et al* (2003) examined δD and $\delta^{13}C$ values of feathers of hummingbirds inhabiting the Ecuadorean Andes and found good agreement between actual and predicted feather δD based entirely on a global model. As expected, feather $\delta^{13}C$ values increased with altitude. Thus, for any given species, it should be possible to estimate approximate elevations at which feathers and other tissues were grown. By examining different tissues with different windows of isotopic integration, the possibility exists to infer previous altitudinal movements.

Applications of deuterium measurements have also been developed in Europe and Africa. The first depiction of the European growing-season basemap was presented in Hobson (2003) and since then more sophisticated treatments have been presented in Bowen *et al.* (2005). A test of the relationship between feathers and predicted precipitation δD in Europe was presented in Hobson *et al.* (2004c) and that study revealed little difference between the relationship derived using growing season or annual precipitation δD. In addition, a poorer relationship was found with these regressions compared to similar work conducted in North America. Nevertheless, some valuable work has already been published based on the European picture

Bearhop *et al.* (2005) used feather and claw δD measurements to distinguish between those Blackcaps *Sylvia atricapilla* breeding in Germany that had wintered in the United Kingdom and those that had wintered in Spain. The overwintering of this species in the UK is a relatively recent phenomenon encouraged by changes in climate and the provisioning of overwintering birds by feeders. The consequences of this 'new' wintering population was that, compared to the more traditional Spanish wintering birds, those wintering in Britain arrived in Germany earlier and tended to mate with others from the same wintering grounds. This 'assortative mating' provides the conditions for speciation and was elegantly quantified using only δD measurements. Other investigations in Europe have inferred the origins of irruptive species to western Europe like Northern Bullfinches *Pyrrhula pyrrhula* (Newton *et al.* 2006) and, more recently, Common Crossbills *Loxia curvirostra* (Marquiss *et al.* 2008). The crossbill study was able to contrast origins of individuals from several irruptions to Scotland over a 100-year period using feathers from museum specimens. More recently, Lormee, Hobson, and Wassenaar (unpubl. data) are investigating the origins of hunter-killed Wood Pigeons *Columba palumbus*

in France using feather δD measurements. That study is designed to establish important baseline information to help manage the hunt of this species in Europe.

The deuterium basemap for Africa shows rather dramatic changes seasonally. However, an interesting and potentially very useful feature is the more depleted values in the southern part of the continent and the extremely enriched region in the northeast, centred on Sudan and Ethiopia. In their investigation into potential wintering sites of the endangered Aquatic Warbler *Acrocephalus paludicola*, Pain *et al.* (2004) did not find δD measurements to be particularly useful, and instead advocated the use of δ¹⁵N and δ¹³C measurements to define wintering areas in Africa. On the other hand, Yohannes *et al.* (2005, 2007) investigated δD together with δ¹⁵N and δ¹³C measurements in feathers of several migrant passerines moving through east Africa where some of them stop to moult *en route* to more southern wintering areas. In these studies, δD measurements were useful in segregating among locally moulting birds and those that delayed their moult until reaching their final (southern) destinations. One of the challenges in applying the δD approach in Africa will be to determine which rainfall matters in terms of regional and local foodwebs and it may well be that depictions of mean annual precipitation δD isoscapes are less useful than those based on more seasonal periods.

The deuterium challenge

Wassenaar and Hobson (2003, 2006) have alerted researchers to the need for careful laboratory protocols when running keratin samples for measurement of δD. Careful adherence to these suggested lab protocols should result in reproducibility of the order of $\pm$ 2 per mil for this isotope. Beyond issues related to measurement error, there is the issue of the appropriate precipitation to feather (or other keratin) δD discrimination factor that should applied to our data in order to create expected keratin δD surfaces or basemaps (Lott and Smith 2006). For songbirds, a value of -25 ‰ has been suggested (Hobson 2005a). That value also seemed appropriate from a regression of feather δD against growing-season average precipitation δD for birds sampled across a large gradient in latitude in North America (Clark *et al.* 2006). Recently, Langin *et al.* (2007) provided additional support for this discrimination factor based on δD measurements of adult American Redstart feathers of known origin. However, such an isotope discrimination factor is almost certainly not applicable to all birds or other species in all situations. In their analysis of songbird feathers from Europe, Hobson *et al.* (2004b) derived a different relationship between feathers and growing-season precipitation δD, albeit based on birds where origin of feather growth was only assumed and not proven. Also, in their extensive survey of raptors across North America, Lott and Smith (2006) determined that their estimate of precipitation to feather δD discrimination value was generally much more positive than that derived for songbirds and showed evidence of geographical variation. Where possible, recent advances in error propagation in assignment of birds to origin based on an honest assessment of variance is now recommended over the use of feather δD discrimination values (Wunder and Norris 2008).

In some ways it is not at all surprising that estimated tissue to precipitation net discrimination factors for δD will vary. First, hydrogen is an element that will exchange with weak O-H or N-H bonds and this can take place with drinking water and overall body water (Hobson *et al.* 1999). Secondly, we know that body δD values can increase as a result of heat stress (McKechnie *et al.* 2004) and presumably as a function of work or high metabolism that results in increased body evapotranspiration. Powell and Hobson (2006) found that Wood Thrush *Hylocichla mustelina* growing feathers in Georgia had higher feather δD values than expected from the feather δD basemap and speculated that heat stress during moult may have been a factor. It is possible that feathers of birds grown in the nest may differ from those of the adults feeding them due to differences in metabolism, drinking water, thermal regime and diet. Langin *et al* (2007) found evidence that feathers of young redstarts indeed differed from those of adults.

Another issue involves our general poor understanding of *which* rainfall matters. The good relationship obtained between feather δD and mean annual growing season δD in North America (Hobson and Wassenaar 1997) was for *forest* birds distributed through the central region of the continent. Closed-canopy forest with shallow root systems may well integrate foodweb δD available to birds and other animals over such long time periods. However in arid areas rainfall driving local foodwebs can occur in just a month or two and different seasonal rains can drive different components of the foodweb (Ehleringer *et al.* 1991).

For birds, moult patterns are reasonably well known for most species. However, stable isotope measurements themselves have provided important qualifiers. The moult of flight feathers of northern populations of the Loggerhead Shrike are essentially bimodal, with inner primaries, secondaries and tail feathers usually being moulted on the breeding grounds but other feathers being grown on the wintering grounds following a suspension in moult, a pattern discovered 'accidentally' using stable isotope measurements (Perez and Hobson 2006). Other birds undergo pre-alternate moult of some body feathers on the wintering grounds prior to migration allowing us to investigate aspects of winter origins or habitat use (Mehl *et al* 2005, Mazerolle *et al.* 2005). Unfortunately, information on the reliability or extent of pre-alternate moult or on the extent of delayed moult in migrating birds is more often not available (Hobson *et al.* 2000). Another alternative is to use claws which are continuously growing. Birds captured soon after their arrival on the breeding grounds should have claws that have retained information from the wintering grounds (Bearhop *et al.* 2003, 2004; Mazerolle and Hobson 2005; Bearhop *et al.* 2005).

Future directions

While emphasis has been placed on isotopic tracers of migratory birds, significant advances in both endogenous and exogenous tracers are expected in the coming years. Undoubtedly, very significant advances will be made on the technological front that will permit remote tracing of smaller and smaller species. Similarly, advances in DNA analyses will involve the rapid description of large sections of the genome of individuals and this will result in the realization of spatial genetic structure in populations previously unimagined. On the stable isotope front a number of advances are expected, based on careful experiments (Gannes *et al.* 1997). Captive rearing experiments are needed that will pay far more attention to the composition of diets with a view to replicating as closely as possible the nutritional range experienced by migrating animals of interest (e.g. Pearson *et al.* 2003). This is especially needed for δD and $\delta^{18}O$ for which virtually nothing is known about physiological and dietary factors determining the isotopic composition of avian tissues.

The ideal situation to infer origins of migratory animals from isotopic analyses of their tissues will be to have as complete an idea as possible of the isoscape from which that animal's tissue were derived. This includes, most importantly, a good sense for the degree and causes of variation for single locations. At present, this includes as a minimum, estimates of variance in isotope values among individuals from known locations for each tissue of interest, within tissue variance, lab measurement error, and an estimate of the error associated with the isoscape model being used (Wunder and Norris 2008).

There are challenges in integrating spatial demographic data with isoscapes to arrive at a continuous picture of migratory connectivity. However, we are typically more interested in migratory dispersal and connectivity *among* populations. That is, the rates at which demographic units exchange individuals (Salomonson 1955, Webster *et al.* 2002). These rates can often be estimated with more certainty than can the geographic coordinates from which an individual originated. However, most previous studies of migratory connectivity have used artificially defined regions or populations to develop assignment likelihoods (Kelly *et al.* 2005). Few studies have attempted to add demographic parameters to their models.

There are numerous possible intrinsic and extrinsic markers that can provide geographic information. It follows that the certainty of assignment of a migrant's origin will likely be

Table 1. Summary of various techniques used to track movements in birds (From Hobson and Norris 2008).

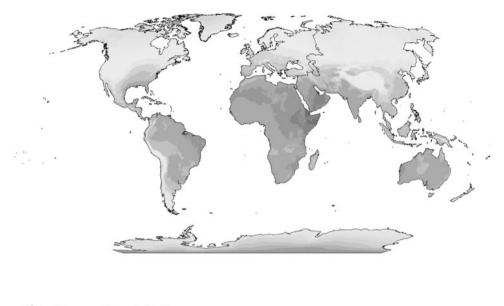| Technique	Advantages	Disadvantages	Key References
Extrinsic	1. Can apply to a broad range of birds. 2. High spatial resolution.	1. Requires initial capture and then recapture or relocation. 2. Biased towards initial capture population.	
Phenotypic variation	1. Inexpensive. 2. Can be applied to historical specimens with high degree of confidence.	1. Low spatial resolution. 2. Not applicable to all species. 3. Provides estimate of natal origin only.	Ramos (1983) Ramos and Warner (1980) Bell (1997) Boulet and Norris (2006)
Ringing/marking	1. Inexpensive. 2. Provides exact information on start and end of movements.	1. Typically low recovery rates. 2. Can take many years to get adequate data. 3. Limited number of major banding stations across globe. 4. Biased towards locations of major recovery stations.	Brewer *et al.* (2000) Bairlein (2001) Berthold (2001)
Radio transmitters	1. Precise locations possible. 2. Precise trajectory if within range of transmission.	1. Low range. 2. Expensive. 3. Adverse effect on behaviour?	Vega-Rivera *et al.* (1998) Cochran *et al.* (2004)
Satellite transmitters	1. Precise animal trajectory.	1. Expensive. 2. Constrained to large animals only (~300 g), 3. Adverse effect on behaviour?	Britten *et al.* (1999) Hays *et al.* (2001) Berthold *et al.* (2002)
ICARUS Project	1. Applies to large number of species. 2. Precise movements and trajectories. 3. Inexpensive following start-up investment.	1. Huge start-up investment. 2. Not yet proven technology. 3. Adverse effect on behaviour?	Wikelski *et al.* (2007)
Passive radar	1. Coverage over large geographic area. 2. Inexpensive. 3. Individuals do not have to be captured.	1. Coverage only from existing stations or portable instruments. 2. Poor ability to determine species- and individual-specific movements.	Bruderer (1997) Gauthreaux and Belser (2003)
Transponders	1. Small transponder size.	1. Requires external (radar/microwave) activation. 2. Low range. 3. Coverage only from existing stations or portable instruments.	Riley *et al.* (1996)
Archival geolocation tags	1. Infers animal trajectory. 2. Light weight (as low as 1.5 g), 3. Inexpensive.	1. Individuals must be recaptured to download data. 2. Accuracy relative to satellite tags still low (approx. 200 km).	Shaffer *et al.* (2005, 2006)
Intrinsic	1. Not biased to initial capture population. 2. Less labour intensive than most extrinsic methods. 3. Every capture produces information.	1. Biased to final captured population (can be overcome by comprehensive sampling coverage). 2. Typically lower resolution than extrinsic markers.	Hobson (1999a) Webster *et al.* (2002), Rubenstein and Hobson (2004)

Table 1. Continued.

Technique	Advantages	Disadvantages	Key References
Contaminants	1. Potentially high spatial resolution (e.g. Mirex).	1. Lack of *a priori* maps of distribution and relative abundance. 2. Distribution of containments may vary predictably over geographic areas. 3. Potential transport of contaminants may dampen or provide unreliable geographic signal.	Braune and Simon (2003) Ochoas-Acuna *et al.* (2002)
Parasites	1. High spatial resolution possible.	1. Species specific? 2. Expensive (via DNA analyses).	Fallon *et al.* 2006
Genetics	1. Several markers possible, 2. East vs. west resolution of migratory fauna in North America.	1. Species specific. 2. Typically low resolution. 3. Provides estimate of natal origin only.	Smith *et al.* (2005) Kelly *et al.* (2005) Boulet *et al.* (2006)
Trace elements	1. Simultaneous measurement of a large number of elements. 2. Potentially high spatial resolution.	1. Lack of *a priori* maps of distribution and relative abundance. 2. Expensive. 3. May require sampling of all possible populations. 4. Evidence that some elements may be integrated into metabolically inactive tissues after growth is complete.	Parrish *et al.* (1983) Kelsall (1984) Szep *et al.* (2003) Norris *et al.* (2007)
Stable isotopes	1. Inexpensive. 2. Not species or taxon specific. 3. Multiple isotopes can be combined to increase spatial resolution. 4. Multiple tissues can provide different time periods of spatial inference.	1. Often low resolution. 2. Lack of isotopic basemaps for several elements and regions. 3. Animal physiology may influence δD values of body water and so complicate interpretations.	Hobson and Wassenaar (1997) Chamberlain *et al.* (1997) Hobson (1999a, b, 2005a, b) Norris *et al.* (2006) Hobson and Wassenaar (2008)

improved by linking isotopic patterns with geographic information from other sets of intrinsic or extrinsic markers. While the ability of each of these markers to provide geographic information is well established, there has been little rigorous work on defining the limits of resolution for each technique or assessing the possible benefits of combining multiple markers. Evaluating the limitations of each combination of intrinsic markers will be important for understanding which types of questions are best addressed with which combinations of markers. A related possibility is the use of extrinsic markers to study and validate patterns in intrinsic markers. The potential to combine innovations in intrinsic and extrinsic markers to track individuals and populations opens a wide array of exciting research questions that to date have been impossible to address. The rarity of such studies to date reflects the degree to which technological hurdles prevent most researchers from employing this strategy.

The number of genetic markers for which it is possible to examine geographic patterns is enormous. Previous research has relied on mitochondrial DNA phylogeography. It seems likely
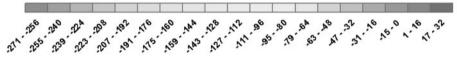
δ²H of Annual Precipitation

Figure 1. Depiction of annual global precipitation δD averaged over International Atomic Energy Agency (IAEA) Global Network of Isotopes in Precipitation (GNIP). From Gabe Bowen's website Waterisotopes.org.

that patterns detected with these markers could be improved through use of amplified fragment length polymorphisms and single nucleotide polymorphisms (Bensch *et al.* 2006). Genetic data, by definition, are not continuous but rather are categorical. For this reason the integration of genetic and isotope data in geospatial analyses has lagged development in these separate fields. Progress will require collaboration between isotopists and geneticists with expertise in geospatial modelling.

To date, trace element profiles, where a suite of elements are measured for relative abundance have shown significant variation among subpopulations. This will assist in tracking species that congregate in a few breeding or wintering sites. Problems arise for cases where species are more diffusely spread across their ranges. Here we face the problem of having little *a priori* information on existing or expected elemental profiles corresponding to origins. Clearly, what is now required is a much closer collaboration between researchers of animal migration and geologists or earth scientists familiar with regional or continental patterns of trace elements.

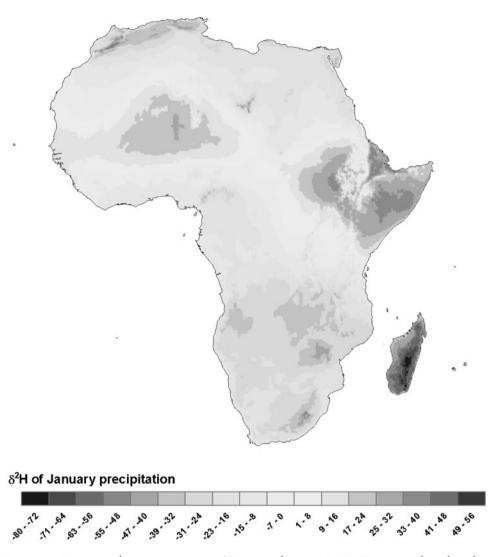## Acknowledgements

δ^2H of January precipitation

Figure 2. Depiction of mean precipitation δD averaged over IAEA GNIP stations for Africa for January. From Gabe Bowen's website Waterisotopes.org.

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