CHAPTER SIX

Emerging Techniques for Isotope Studies of Avian Ecology*

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Abstract. Stable isotope analysis has expanded the usefulness of avian specimen collections in ways that were generally unanticipated by the original collectors. This technique enables aspects of avian ecology to be studied using very small samples of feather or other tissue taken from specimens. Stable isotope values can be informative about diet, trophic ecology, spatial habitat use, and the migratory connectivity of breeding and nonbreeding populations. They can also provide access to understudied time periods in a bird's annual cycle, particularly periods of molt. Use of museum specimens offers advantages for these studies: museum collections generally span longer time periods than field samples and represent broad geographic ranges. In this chapter, we review established and emerging isotopic techniques and their applications in avian ecology, with an aim to inspire and inform research using museum collections. We focus on analyses of bulk tissues and proteins, and we discuss ways in which sampling strategies for museum specimens can be adjusted to suit the research question, including considerations such as the timing of feather molt and the length of time during the life of a bird that is reflected by a sample. We also discuss general caveats for interpreting isotope data, the variance of which is usually influenced by multiple factors. In greater detail, we present recommendations for sampling museum specimens, such as avoiding a potential confounding influence of melanin concentration on carbon isotope values in feather, and minimizing damage to museum specimens when sampling. Stable isotope data from museum specimens have great potential to inform ornithologists about the trophic and spatial ecology of birds, and to provide long-term baseline data for studying how these attributes may be changing in the Anthropocene.

Key Words: bird, carbon isotope, diet, feather, foraging, hydrogen isotope, migration, nitrogen isotope, seabird.

Stable isotope analysis is now used to address a broad range of research topics in avian ecology and physiology, from the migratory connectivity of songbird populations and the source of nutrients that females provision to eggs, to the spatial and trophic ecology of seabird communities (Rubenstein and Hobson 2004, Inger and Bearhop 2008). Stable isotope-based research has been used in ornithological research since the 1980s (Minagawa and Wada 1984, Schoeninger and DeNiro 1984, Hobson 1987) and has grown steadily in abundance since the

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late 1990s (Figure 6.1). While a small proportion of those studies have incorporated samples from museum specimens, we see great potential to enhance ornithological knowledge by more fully employing museum collections.

In the most general terms, stable isotope analysis is useful in the study of birds because the isotopic composition of avian tissues can reflect aspects of diet, geographic location, habitat, or physiology, depending upon the chemical element studied. This approach is based on the observations that (a) the isotopic composition of bird tissues is similar to, or differs predictably from, diet or drinking water; and (b) that there are consistent geographic and physiologically driven patterns in stable isotope ratios. As intrinsic markers, stable isotopes can be used to study aspects of bird ecology that are difficult or impossible to observe directly, including the migratory patterns of rare or otherwise difficult-to-track populations and the former diets and habitats of extinct species (Hobson and Montevecchi 1991, Chamberlain et al. 1997, Cherel et al. 2006, Clark et al. 2006). Stable isotope analysis also holds practical appeal due to its relatively low per-sample cost, in terms of both time and money, and because samples required for most isotope analyses are very small (e.g., 1 mg) and can thus be taken with minimal effects on live birds or museum specimens. For these reasons, stable isotopes are often useful companions to more expensive and invasive techniques, such as satellite tracking and dietary studies that rely on forced regurgitation or sacrifice of the animal for stomach content analysis (Meckstroth et al. 2007, Votier et al. 2010, González-Solís et al. 2011).

Museums can be a critical sample resource for isotope-based studies of avian ecology. Museums often hold specimens collected from across a species' geographic range, which can be particularly valuable to developing an understanding of spatial isotope patterns, for example, to understand connectivity between widely dispersed breeding and nonbreeding populations of migrants (Kelly et al. 2002, Lott et al. 2003). In addition, museum collections often hold specimens that are difficult or impossible to sample in the field because they are from rare, logistically difficult to access, or extinct species. Indeed, historically collected or archaeological and paleontological specimens provide particularly exciting samples to isotope researchers, who can use them to reconstruct historical trends in ecology (e.g., Thompson et al. 1995, Becker and Beissinger 2006, Wiley et al. 2013). Ornithologists today are faced with a pressing need to characterize and preserve diminishing avian biodiversity. This task involves understanding the nature and scope of human impacts on bird populations over timescales ranging from decades to millennia. Museum specimens are a source of samples that span these broad temporal scales, and the stable isotope ratios of organic matter preserved within these specimens provide a means of documenting shifts in foraging ecology, environmental biogeochemistry, and physiology. Stable isotope data can therefore make valuable contributions to the extended specimen

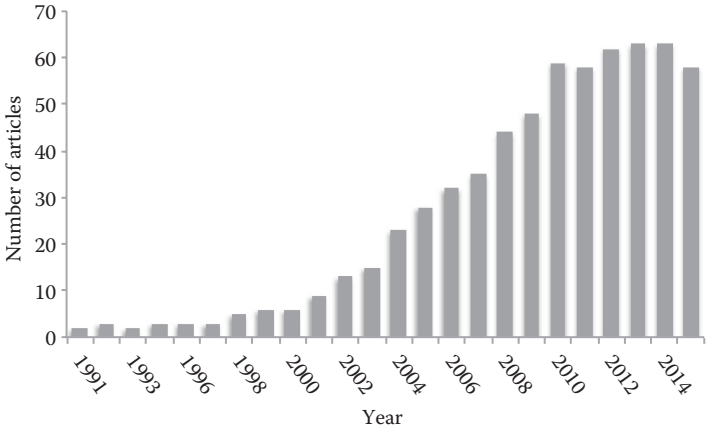

Figure 6.1. Published articles with key words "stable isotope" and "bird" within the Web of Science, by year. (Modified from a Web of Science citation report created December 15, 2015.)

(Chapter 1, this volume); they can both elaborate on the phenotype of individuals represented in museum collections and describe the ecological context from which birds were sampled.

This chapter is written to both inspire and inform the use of museum specimens in stable isotope-based studies of birds. To date, these studies have predominantly focused on isotope data from proteins and whole tissues; this chapter is similarly focused. For readers new to the field of isotope ecology, we include a brief section introducing stable isotope methodology and a section exploring applications of stable isotopic data in ornithology. We do not attempt to cover all studies in this large and growing field, but rather provide selected examples to capture its breadth, complications, and possibilities. With respect to museum specimens, we include a section on the challenges of using stable isotope techniques and sources of interpretation errors, and another section on sampling considerations and strategies, highlighting examples from our own research on procellariiform seabirds. This latter section places a heavy emphasis on the feather, as it is the most readily available tissue from museum specimens and is by far the most commonly used for isotope studies. Finally, we discuss challenges and recommendations for future isotope studies, and we propose ways in which the utility of museum collections could be increased for isotope researchers.

STABLE ISOTOPES: BASIC THEORY AND METHODOLOGY

Stable isotopes are unique forms of an element that differ in neutron number and do not radioactively decay. For example, ^{12}C and ^{13}C are stable isotopes, but not ^{14}C, which decays into ^{14}N through time. Due to the difference in neutron number, stable isotopes of a given element differ from each other in mass and relative abundance. For example, about 98.9% of all carbon atoms on earth are isotope ^{12}C, while only 1.1% are ^{13}C. ^{12}C is therefore referred to as the abundant isotope, while ^{13}C is considered the rare isotope. Although the stable isotopes of an element co-occur in natural substances and participate in the same chemical reactions, the reaction rate constant, or the rate at which a reaction proceeds, is higher for the lighter, typically more abundant, isotope than for the heavier, typically rare, one. Because of its higher reaction rate constant, the light isotope is often enriched in the product of reaction, as compared with the heavy isotope. This phenomenon is referred to as fractionation and is described by a fractionation factor (α), which is the ratio of two reaction rate constants:

$$\alpha = k2/k1$$

where k1 and k2 are the rate constants for the light and heavy isotope, respectively.

Fractionation causes isotope ratios to vary among different organs, organisms, and nonliving substances. For example, plants using C3 photosynthesis incorporate less ^{13}C during CO_2 fixation than do plants with C4 photosynthesis, and so they have less ^{13}C in their tissues than do plants using C4 photosynthesis (Marshall et al. 2007). Biologists have learned to exploit naturally occurring isotopic variation in order to study the flow of elements through ecosystems and organisms, in the process gaining knowledge of food web structure, habitat use, and physiology for a broad range of habitats and species (Fry 2006). Just as C3 and C4 plants differ from each other in the relative abundance of ^{13}C, entire food webs based on these photosynthetic pathways are also isotopically distinct. Similarly, differences between fresh and seawater in the ratio of oxygen's most abundant isotopes, ^{18}O and ^{16}O, are incorporated into animal tissues and have been used to infer populations' relative use of those water sources (Schaffner and Swart 1991, Clark et al. 2006).

Stable isotopes of the "light" elements—C, N, H, O, and S—are most commonly used to study bird ecology. Isotope data are reported in delta notation as $\delta^{13}C$, $\delta^{15}N$, δD (or $\delta^{2}H$), $\delta^{18}O$, and $\delta^{34}S$ values, expressed as ‰ (per mil). Delta notation represents the ratio of isotopes within a substance, as compared to that of an internationally accepted standard:

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1000$$

where X = ^{13}C, ^{15}N, D, ^{18}O, or ^{34}S; and R is the corresponding ratio of the element of interest: $^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{2}H/^{1}H$, or $^{34}S/^{32}S$ (Coplen et al. 1983, Coplen 1994).

Stable isotope measurements are typically made using stable isotope mass spectrometers, which require that the sample be turned into a gas, and then the gas of interest (e.g., CO_2) be purified from

other gas species in the sample. For example, the measurement of $\delta^{13}C$ from bone collagen requires combustion of collagen and purification of CO_2 from other combustion products such as N_2, H_2O, O_2, and SO_x. Purification can be achieved cryogenically, chemically, and/or chromatographically. Within the source of a mass spectrometer, the gas of interest is ionized and then accelerated into a magnetic field. Within the magnetic field, ions are deflected and separated according to their mass to charge ratio (m/z) based on the principle that ions of higher m/z have a greater radius of deflection than those of lower m/z.

In ecological stable isotope studies, researchers are interested in either the analysis of whole or "bulk" organic material such as tissues, proteins, or sediments, or else they are focused on individual compounds such as amino acids and alkanes. The majority of bulk isotope data used in ecological studies is now produced with the aid of an elemental analyzer that combusts and purifies gases (e.g., N_2, CO_2) from a small aliquot of liquid or solid. A stream of helium (He) serves to move the sample gas through the elemental analyzer and into the mass spectrometer for isotope analysis. The analysis of individual compounds or compound specific isotope analysis (CSIA) first requires the compound class of interest (i.e., amino acids, hydrocarbons, fatty acids) to be purified from a mixture. In the case of amino acids derived from collagen, the collagen is purified from the bone mineral and other proteins, and then hydrolyzed to produce free amino acids. If the compound class is not volatile, its constituents must be chemically modified to a volatile form, as is the case with amino acids. The individual compounds in the compound class must be separated on a gas chromatograph (GC) prior to combustion and isotope analysis. Thus, the sample is injected into a GC where it is carried onto a column and, ultimately, to the mass spectrometer by a stream of He. After separation on the GC column, compounds move, individually, into a furnace where they are combusted. The combustion gases are then cryogenically purified into the gas of interest prior to entering the mass spectrometer for isotope analysis.

AVIAN SPECIMENS IN STABLE ISOTOPE ECOLOGY

Stable isotope studies in ornithology can be considered a subdiscipline within a field often referred to as stable isotope ecology, which is itself a large and expanding discipline. Several excellent reviews are available for readers interested in the broader field of stable isotope ecology and further discussion of ornithological applications (Rubenstein and Hobson 2004, Fry 2006, West et al. 2006, Inger and Bearhop 2008, del Rio et al. 2009, Boecklen et al. 2011). Here, we discuss the well-established applications of stable isotopes in ornithology and highlight those that are most likely to involve museum specimens.

Two of the most productive areas of isotope-based ornithological research include studies of diet composition and spatial habitat use. Such studies are founded on the principle that the isotope value of a bird's tissues typically reflects the isotope value of its diet (or diet and drinking water, in the case of H and O), plus a predictable offset. This offset is often referred to as a discrimination factor. For example, the offset between local precipitation and a given animal's tissue is referred to as a precipitation-to-tissue discrimination factor, whereas the difference in isotope value between an organism, or its tissue, and its diet is called a trophic discrimination factor (TDF). Controlled feeding experiments can delineate the TDF for different tissues and demonstrate a predictable relationship between a bird and its diet, facilitating dietary studies for wild bird populations (e.g., Hobson and Clark 1992a,b, Hobson and Bairlein 2003, Cherel et al. 2005, Federer et al. 2010). Although isotope-based studies of bird diet can only differentiate between foods that are isotopically distinct, there are a range of variables that cause avian diets to differ from one another, including trophic level, ecosystem or habitat type, and spatial position; spatial patterns in isotope values are often referred to as isoscapes. In Table 6.1, we detail sources of stable isotope variation that have been used as the basis for avian studies. Although nonexhaustive, this list demonstrates the diversity of factors contributing to stable isotope variation in birds and their diets, and the corresponding diversity of ornithological research that is possible with stable isotope techniques.

The types of questions that isotope-based studies can address expands further when you consider that different bird tissues provide information from distinct timescales (see Table 6.2; Dalerum and Angerbjörn 2005). Among metabolically active tissues, the rate of turnover varies such that isotope values can reflect periods as short as

TABLE 6.1

A nonexhaustive list of sources or interpretations of stable isotope variations in bird tissues.

δ value	Environment	Source of variation	Example studies
$\delta^{13}C$	Marine	Foraging latitude	Cherel and Hobson (2007), Jaeger et al. (2010)
		Benthic versus pelagic food webs	Hobson et al. (1994)
	Terrestrial	C3 versus C4 versus CAM-based food webs; mesic versus xeric habitats	Marra et al. (1998), Bearhop et al. (2004), Clark et al. (2006)
	All	Incorporation of dietary lipids into tissue protein	Thompson et al. (2000)
	Mixed	Marine versus terrestrial C3/freshwater	Tietje and Teer (1988), Hobson and Sealy (1991), Gunnarsson et al. (2005)
$\delta^{15}N$	Marine	Foraging location (spatial variation in N cycling, e.g., denitrification)	Cherel et al. (2000), Wiley et al. (2012)
	Terrestrial	Mesic versus xeric habitats	Sealy et al. (1987), Ambrose (1991)
	All	Anthropogenically fixed N additions (fertilizer use)	Hebert and Wassenaar (2001)
		Trophic level	Kelly (2000), Becker and Beissinger (2006)
		Food restriction/starvation	Cherel et al. (2005) (but see Graves et al. 2012)[a]
	Mixed	Marine versus terrestrial/freshwater diet	Chamberlain et al. (2005)
$\delta D/\delta^{18}O$	Terrestrial	Geographic patterns in meteoric water (associated with altitude, latitude, and distance from ocean)	Hobson et al. (2001), Hobson et al. (2004), Bearhop et al. (2005), Greenberg et al. (2007)
$\delta^{18}O$	Mixed	Marine versus freshwater use	Shaffner and Swart (1991)
δD	All	Evaporative water loss	McKechnie et al. (2004), Powell and Hobson (2006)
$\delta^{34}S$	Marine	Benthic versus pelagic food webs	Thode (1991)
	Mixed	Marine versus estuarine/marsh versus terrestrial/freshwater diet	Hobson et al. (1997), Thode (1991)

[a] The tendency of food restriction and starvation to elevate $\delta^{15}N$ values appears to vary based on tissue type, with tissues that are actively maintained or synthesized during periods of fasting being most likely to show increased $\delta^{15}N$ (see Martinez del Rio et al. 2008).

days, as in blood plasma, or as long as years, as in bone collagen (Hobson and Clark 1992a, Pearson et al. 2003, Hedges et al. 2007). Isotope data from metabolically inert tissues such as feathers and toenails record information over the period of tissue synthesis, after which time they remain isotopically unchanged (Hobson and Clark 1992a). Understandably, feathers have become a favorite of isotope researchers as they can be sampled with minimal damage to live birds and museum specimens. Additionally, feathers are sometimes grown on distant nonbreeding grounds when birds typically are more difficult to study directly.

Researchers have successfully used the isotopic composition of multiple tissues, including feathers, to study different time periods within the annual cycle and to study intraindividual variation in resource use at a variety of timescales (Dalerum and Angerbjörn 2005). An important caveat is that it can be difficult to directly compare isotope data from multiple tissues: they will differ not only as a function of time, but also in accordance with their unique TDFs. For example, different tissues have distinct amino acid compositions and can be synthesized from different portions of the diet; the disparity in isotope values between diet and tissues (tissue-specific TDFs) tends to vary. Notably, TDFs have been measured for a variety of avian tissues and species, but because TDFs vary among species

TABLE 6.2

Bird tissues commonly used for stable isotope analysis and the time periods they reflect, described by half-life (metabolically active tissues) and growth rates (metabolically inert tissues).

Tissue	Species	Half-life (days)[a]		Source
		$\delta^{13}C$	$\delta^{15}N$	
Blood plasma	American Crow (*Corvus brachyrhynchos*)	2.9	0.7–1.7	Hobson and Clark (1992a)
	Yellow-rumped Warbler (*Setophaga coronata*)	0.4–0.7		Pearson et al. (2003)
Red blood cells	American Crow	29.8		Hobson and Clark (1992a)
Whole blood	Japanese Quail (*Coturnix japonica*)	11.4		Hobson and Clark (1992a)
	Great Skua (*Stercorarius skua*)	14	15.7	Bearhop et al. (2002)
	Garden Warbler (*Sylvia borin*)	11	5–5.7	Hobson and Bairlein (2003)
	Yellow-rumped Warbler	4–6	7.5–27.7	Pearson et al. (2003)
	Dunlin (*Calidris alpina*)	11.2	10	Ogden et al. (2004)
Liver	Japanese Quail	2.6		Hobson and Clark (1992a)
Muscle	Japanese Quail	12.4		Hobson and Clark (1992a)
Bone collagen	Japanese Quail	173.3[b]		Hobson and Clark (1992a)
		Growth rate		
Feather	Various[c]	1.7–11.0mm/day		Prevost (1983)[d]
Toenail	Five Palearctic passerine species	0.04 ± 0.01 mm/day growth rate		Bearhop et al. (2003)

[a] The turnover rate of a particular tissue can vary between species, generally slowing in larger species and species or individuals with lower protein intake (Martinez del Rio et al. 2009).

[b] Although Hobson and Clark (1992a) is the only study documenting bone collagen turnover in birds, other studies suggest that carbon in collagen can reflect decades or even the lifetime of an adult (e.g., Hedges et al. 2007).

[c] Lower range of feather growth rates was reported for the Ashy Storm-Petrel (*Oceanodroma homochroa*), and upper range for the Red-crowned Crane (*Grus japonensis*).

[d] Reports a range of growth rates, as reviewed by Rohwer et al. (2009).

(e.g., due to different dietary protein intake), there is some degree of error when TDFs are extrapolated beyond the original study organisms where they were measured (Cherel et al. 2005, Robbins et al. 2005).

Taking advantage of both a suite of available study variables and timescales, isotope researchers have built a substantial body of literature on avian diet and habitat use. For example, marine and terrestrial organisms generally differ in $\delta^{13}C$ and $\delta^{15}N$, differences that have been used to estimate the marine contribution to the diets of insular Northern Saw-whet Owl (*Aegolius acadicus*) and ancient California Condors (*Gymnogyps californianus*), and to infer a temporal increase in the use of terrestrial food by Herring Gulls (*Larus argentatus*) in the Great Lakes (Hobson and Sealy 1991, Chamberlain et al. 2005, Hebert et al. 2008). $\delta^{15}N$ values are used widely to study the trophic level of birds and food web structure (Hobson et al. 1994, Sydeman et al. 1997, Beaudoin et al. 2001). This tool is the basis of a growing body of literature suggesting that seabirds in both coastal and oceanic regions may have shifted to lower trophic level prey after the onset of industrialized fishing and whaling within their foraging ranges (Becker and Beissinger 2006, Emslie and Patterson 2007, Farmer and Leonard 2011, Wiley et al. 2013). Archived bird specimens were sampled in most of the aforementioned studies, highlighting the value of museum collections in addressing these questions. Isotope research delineating changes in foraging habits through time can play a critical role in understanding avian population declines, and we predict this approach will have a rich future that is closely

tied to museum specimen availability (Norris et al. 2007, Blight et al. 2014).

Stable isotopes also provide insight into bird migration and other spatial movement patterns (Hobson 1999, Webster et al. 2002, Rubenstein and Hobson 2004). The use of hydrogen isotopes to study migration is particularly common. This technique is based on the existence of continental-scale patterns in the δD value of precipitation, which is related to latitude, distance from the ocean, and altitude, and on the observation that birds typically incorporate the δD value of local precipitation into their growing tissues with a predictable offset, or precipitation-to-tissue discrimination factor (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Hobson et al. 2004, Inger and Bearhop 2008). Geographic patterns of precipitation δD values are particularly well-described across continental North America, where feathers collected on the breeding grounds, but grown on the wintering grounds, are now commonly used to infer general wintering location and to help link wintering and breeding populations (Hobson et al. 2001, Bearhop et al. 2005). The utility of this approach is nicely demonstrated in the study by Greenberg et al. (2007), which used δD values to estimate the latitude of previously unknown Coastal Plain Swamp Sparrow (*Melospiza georgiana nigrescens*) wintering locations. With additional insight on the brackish habitat type of the wintering location inferred from feather $\delta^{13}C$ and $\delta^{15}N$, the authors were able to physically locate the wintering population (Greenberg et al. 2007).

Although geographic patterns, or isoscapes, of δD are absent in the ocean, $\delta^{13}C$ isoscapes have been commonly used to infer relative foraging latitude among marine birds (Cherel et al. 2006, Cherel and Hobson 2007, Jaeger et al. 2010). The broad-scale, inverse relationship between $\delta^{13}C$ and latitude throughout the world's oceans results from temperature-induced variation in the concentration of CO_2, which changes the extent to which phytoplankton incorporate ^{13}C during CO_2 uptake (Goericke and Fry 1994). A variety of other spatial patterns in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ have been recognized in marine, freshwater, and terrestrial environments, and these isoscapes can and have been used for studies of movement patterns in a variety of birds (Kelly 2000, Rubenstein and Hobson 2004, Braune et al. 2005, Hebert and Wassanaar 2005, Coulton et al. 2010, Wiley et al. 2012). In some cases, samples from museum specimens have helped to describe isoscapes by increasing their spatial coverage and the rapidity of their development (e.g., Kelly et al. 2002).

As direct electronic tracking of birds becomes more feasible, stable isotopes have often entered into a partnership with tracking data, where isotopes provide increased sample size and the ability to include archived samples from birds that cannot be captured and tagged (Knoche et al. 2007). Although isotope analyses cannot provide the level of spatial resolution that is available through electronic tracking (Robinson et al. 2010, Hedd et al. 2012), they are much less expensive and labor-intensive. Importantly, isotope values often reflect diet in addition to location, meaning they can add a perspective on foraging that is impossible to obtain through tracking. We suggest that, after study systems are well-described by joint isotope-tracking research, stable isotopes may provide a means of cheaply monitoring for changes in a population's movements and foraging habits into the future.

Stable isotopes have provided important advances on a variety of other topics, such as the balance of endogenous versus exogenous nutrient allocation to egg and feather formation (Hobson et al. 1997, Klaassen et al. 2001, Fox et al. 2009, DeVink et al. 2011), the transport of marine-derived nutrients to terrestrial ecosystems by breeding seabirds (Wainright et al. 1998, Stapp et al. 1999), and potential carryover effects on fitness between the period of molt and the breeding season (Marra et al. 1998, Norris and Marra 2007, Kouwenberg et al. 2013). Stable isotopes have also proven useful in studies of habitat segregation between the sexes during the, often understudied, nonbreeding season (Marra and Holmes 2001) and in investigations of variable contaminant and disease exposure (Bearhop et al. 2000, Braune and Hobson 2002, Hobson et al. 2002, Hebert et al. 2014). Each of these studies relied on one or more of the sources of isotope variation listed in Table 6.1.

EMERGING ANALYTICAL TECHNIQUES

Before moving on, we highlight two emerging methods in stable isotope ecology that are growing in influence. First, Bayesian analyses of mass balance models are becoming common in food web studies. Mass balance models, such as Isosource, have long been used in food

web studies to evaluate the relative importance of dietary items to consumers (Phillips and Greg 2003). Bayesian analysis of mass balance models produces estimates of the relative contributions of sources (often prey) to isotope values (often of consumers) as true probability density functions rather than the simple range of possible values that is produced by mass balance models (Parnell et al. 2010). Bayesian methodology also has the advantage that the analyst can incorporate prior knowledge about source contributions to the diet of the animal under investigation, which can increase precision and accuracy of diet estimates (Parnell et al. 2013).

Standard ellipsoid models are an important approach derived from a Bayesian framework (Jackson et al. 2011). The mean isotope values for the population are the center of the ellipse, whereas eigenvalues of a covariance matrix generated from a multivariate normal distribution are used to derive the area of the ellipse (SEA_b). The ellipse defines an area on a bivariate isotope plot and is a reflection of isotopic variation for a population. The ellipse area can also be interpreted as a measure of "isotopic niche width" if isotope values can be clearly related to foraging attributes such as habitat (Newsome et al. 2010, Jackson et al. 2011). Importantly, Bayesian methods can also provide estimates of the probability that two means may be different, rather than confidence intervals provided by frequentist analysis of variance (ANOVA) approaches.

Advances are also being made in the use of compound-specific isotope analysis. This technique generates isotope data from individual compounds such as fatty acids or amino acids, instead of whole tissues or proteins; this latter class of analyses is often referred to as "bulk" isotope analysis. Compound-specific isotope analyses offer the ability to differentiate between otherwise confounded sources of isotope variation. For example, $\delta^{15}N$ values are commonly used to infer relative trophic position, but spatial variability in $\delta^{15}N$ values (e.g., from differences in the relative use of nitrate versus atmospheric N_2 at the base of marine food webs) can confound interpretations of trophic position. Some amino acids, such as phenylalanine (Phe), are incorporated from diet into consumer tissues with negligible TDFs and have $\delta^{15}N$ values that predominantly reflect the nitrogen source, that is, the $\delta^{15}N$ of nitrogen used by primary producers at the base of the food web. Other amino acids, such as glutamic acid (Glu), have large TDFs and therefore show isotopic shifts due to trophic transfers, in addition to reflecting source nitrogen $\delta^{15}N$ (McClelland and Montoyo 2002, Chikaraishi et al. 2009). By comparing the $\delta^{15}N$ value of Phe and Glu (or other so-called source and trophic amino acids), researchers are able to distinguish between variation in trophic level and variation in nitrogen source (Choy et al. 2012, Steffan et al. 2013). This amino acid-specific $\delta^{15}N$ technique offers another exciting prospect: the potential to generate reliable estimates of trophic level for individual birds in the absence of prey or primary producer samples. However, accurate trophic level estimates of birds will require further experimental work that clearly defines the TDF for amino acids in avian tissues (Lorrain et al. 2009, McMahon et al. 2015).

POTENTIAL CONFOUNDING FACTORS AND OTHER SOURCES OF ERROR

Stable isotopes can be powerful tools, but interpretation of isotope data can be challenging, as the ratio of isotopes for any given element can vary as a function of multiple factors. It is the responsibility of every thoughtful isotope researcher to understand the potential sources of isotope variation within their study system as well as the assumptions of isotope methods that, when violated, may be sources of interpretive error. For example, many isotope studies assume that birds are in isotopic equilibrium with their food sources, such that newly formed tissues will reflect the present diet and location. This assumption is not always met. Birds may retain metabolic pools derived from previous locations and may catabolize previously built tissues in order to synthesize new ones; this has been highlighted by isotope studies of exogenous versus endogenous reserves in egg and feather formation (Klaassen et al. 2001, Fox et al. 2009).

We do not attempt to summarize all potential sources of error here, but note that careful consideration of spatial and temporal scale is imperative. For example, δD isoscapes can be powerful indicators of long-distance movements, but at small spatial scales, δD variation may predominately derive from factors other than geographical location because of isotopic influences from local hydrology or water lost from birds' bodies through evaporative cooling (Powell and Hobson

2006, Wunder et al. 2012). Similarly, isoscapes do not always preclude the possibility that bird tissues with similar isotope values were formed in very distant locations. Just as researchers should carefully consider the limitations of isoscapes, they should also acknowledge limits in temporal resolution. For example, the precise timing of feather growth is often unknown, even when molt sequence and season have been described, and intraspecific variation in the timing of feather growth can sometimes explain significant isotope differences (e.g., Wunder et al. 2012).

The occasional discovery of new sources of isotope variation in bird tissues highlights our sometimes-incomplete understanding, but, at the same time, it can inspire the development of new isotopic research tools. For example, Ostrom et al. (2014) discovered a range of >100‰ in δD values among seabirds foraging in the open ocean, even though δD values of water and potential prey are relatively invariant. They hypothesized that isotopic discrimination associated with salt excretion via nasal salt glands is the main cause of this variability, and that birds that eat salty invertebrates as opposed to less salty teleost fish tend to have higher δD values. Further work is needed to determine if δD is a useful tool for studying diet in birds with well-developed salt glands.

Studies uncovering new sources of isotope heterogeneity may also alert us to potentially confounding factors that can be better controlled in future research. For instance, Michalik et al. (2010) and Wiley et al. (2010) found that feather containing the pigment eumelanin tends to be depleted in ^{13}C relative to melanin-free feather (Figure 6.2). This effect may result from the synthesis of eumelanin from the amino acid tyrosine, which is incorporated into avian tissues from diet with little or no biochemical alteration, and is itself depleted in ^{13}C relative to bulk keratin (McCullagh et al. 2005). Similarly, Grecian et al. (2015) showed an offset in $\delta^{13}C$ between feather vane and feather rachis, which they attributed to a difference in amino acid composition between these two feather components. Regardless of cause, these findings demonstrate that consistency in sampling technique can be important, and isotope researchers should continue to explore isotopic heterogeneity within bird populations, individuals, and tissues to test assumptions of their techniques.

When sampling museum specimens, researchers should also consider the possibility that preservation methods may have altered the original isotope values of avian tissues. Most published research on this topic has concentrated on the

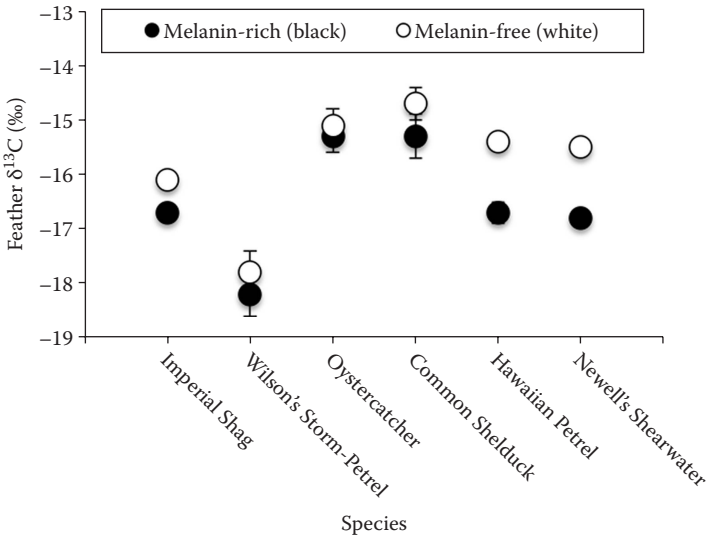

Figure 6.2. Stable carbon isotope values of melanin-rich and melanin-free feathers in six species. Data points represent group means ± standard errors. (Imperial Shag [*Phalacrocorax atriceps*], Wilson's Storm-Petrel [*Oceanites oceanicus*], Oystercatcher [*Haematopus ostralegus*], and Common Shelduck [*Todorna tadorna*] data are from Michalik et al. 2010. Hawaiian Petrel [*Pterodroma sandwichensis*] and Newell's Shearwater [*Puffinus auricularis newelli*] data are from Wiley et al. 2010.)

use of ethanol and formalin-preserved specimens. Several studies found no impact of ethanol preservation on $\delta^{13}C$ and $\delta^{15}N$ values, and a consistent, and therefore correctable, impact of formalin on $\delta^{13}C$ (Sarakinos et al. 2002 and citations therein, Barrow et al. 2008). However, Kaehler and Pakhomov (2001) and Kelly (2006) found that ethanol can sometimes alter $\delta^{13}C$ values of preserved organisms, and the effects of ethanol and formalin can apparently vary between species and tissue types (e.g., Sweeting et al. 2004). Taken together, these studies suggest that investigators should carefully consider methods of sample preservation and may need to carry out experiments to test the equivalency of preservation methods (e.g., drying versus freezing versus ethanol and formalin preservation) for the particular taxa and tissues of interest.

The list of potentially confounding factors in stable isotope studies may be daunting to new isotope users. However, we note that multiple isotopes can often be used to constrain potential sources of variation and afford more definitive conclusions (Lott et al. 2003). In other cases, ground-truthing with conventional, nonisotopic techniques can provide a foundation for isotope-based inferences (González-Solís et al. 2011). Knowledge of a species' natural history can also be a means of discounting potential sources of isotope variation. Finally, we echo a conclusion made by Inger and Bearhop (2008): although potential sources of error in isotope-based studies of birds exist, many can be overcome simply by thoughtful study design.

STRATEGIES FOR SAMPLING MUSEUM SPECIMENS

For any isotope-based study of birds, one of the first decisions about sampling will be the choice of tissue type. Avian museum specimens are most commonly sampled for feather and bone. Bone has generally been used in studies of zooarchaeological and paleontological samples, which tend to rely on isotope data from collagen, the dominant bone protein. A much larger number of studies have used feathers. To illustrate the different utilities of these two tissues, we present data from the Hawaiian Petrel (*Pterodroma sandwichensis*) as a case study.

Thanks to the abundant ancient bone record of the Hawaiian Petrel, Wiley et al. (2013) were able to construct isotope timelines reaching back circa 4,000 years (Figure 6.3). These timelines reflect

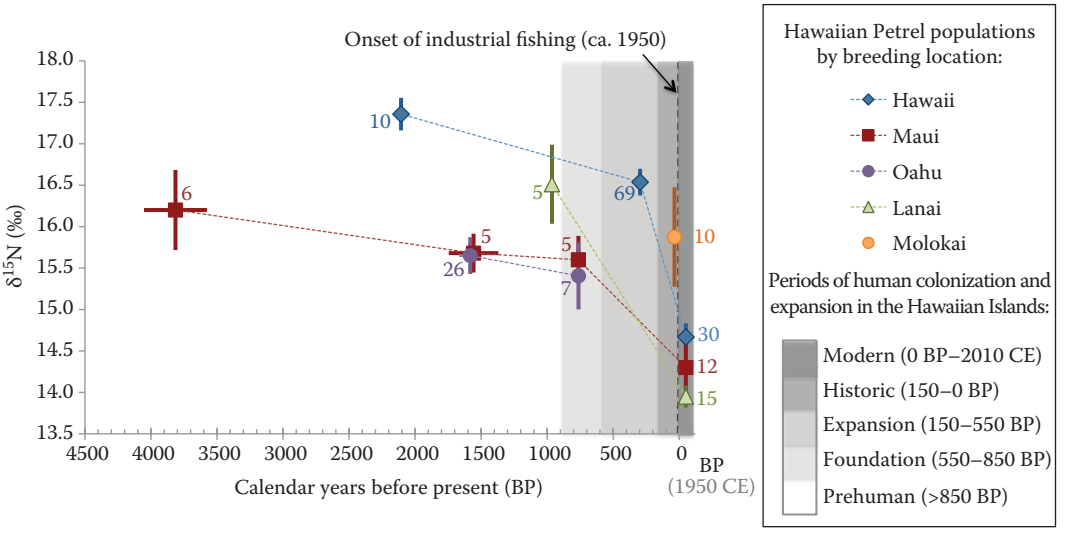

Figure 6.3. Isotope data from bone collagen provide time-averaged signals of diet and the possibility of constructing historic and prehistoric timelines. Here, $\delta^{15}N$ values of modern and radiocarbon-dated bone collagen are shown for five Hawaiian Petrel populations. The average age and isotopic composition of each time bin, ± standard error, is plotted with sample size noted. Gray shading indicates time bins. Modern samples were unavailable from Oahu and Molokai due to population extirpation. Stippled lines connecting data points are for visualization purposes; isotopic shifts between time bins may have occurred nonlinearly. CE, Common Era. (Reprinted with permission from Wiley et al. 2013.)

an integrated measure of diet over the course of the annual cycle, and likely over months to years in the life of each individual bird. Such time-averaged signals can be ideal for studies covering large temporal scales. Hawaiian Petrel $\delta^{15}N$ values show a striking pattern of decline through time, with all significant change isolated to the interval between the two most modern time bins in three populations. Wiley et al. (2013) interpreted this $\delta^{15}N$ decline as most likely reflecting a decline in trophic level: perhaps a shift in petrel diet caused by the onset of industrial fishing. Such a decline was previously undocumented for a tropical, open ocean predator, and suggests potentially widespread changes in Hawaiian Petrel food webs, which extend from the equator to near the Aleutian Islands. Importantly, the Hawaiian Petrel isotope chronology includes data from well before the advent of humans in the breeding grounds or foraging range of the species. These data therefore establish a prehuman baseline for an endangered seabird, against which modern and future data can be compared.

In contrast, Wiley et al. (2014) use stable carbon and nitrogen isotope data from Hawaiian Petrel feathers to detail modern foraging diversity (Figure 6.4). Whereas collagen data do not show significant differences among modern petrel populations, data from flight feathers grown during the chick-rearing period (by hatch-year birds) and nonbreeding season (adults) are consistent with differences in foraging location between populations and also between periods of the annual cycle (Wiley et al. 2014). These data provide concrete guidance on how to collect electronic tracking data that represent the species as a whole. For example, it is clear from isotope data that Maui Petrels, previously tracked during the breeding season, likely provide different results than would tracking of any population into the

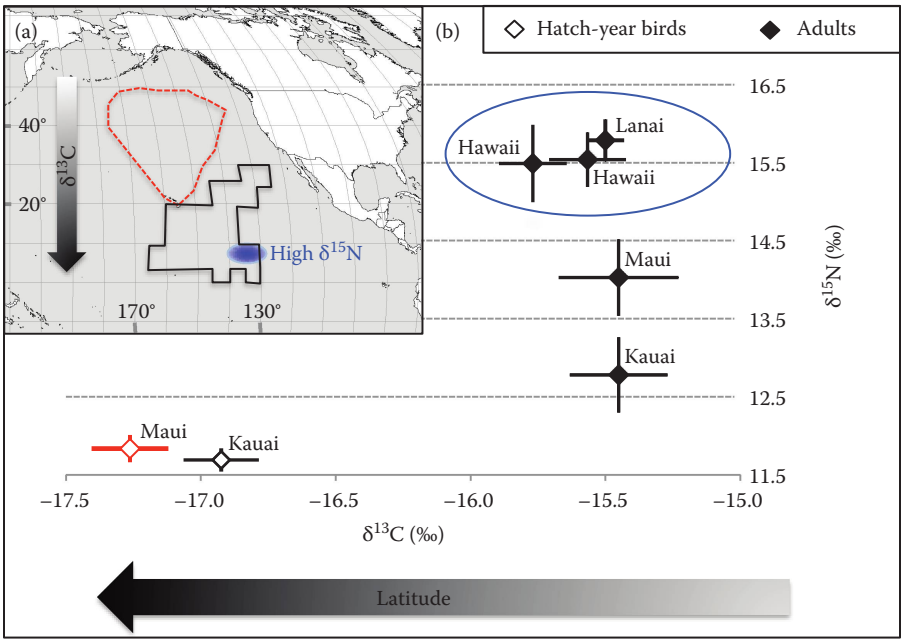

Figure 6.4. Feather data can provide insight into foraging ecology over multiple, discrete periods of the annual cycle. Here, flight feather isotope data are shown alongside at-sea locations of Hawaiian Petrels. In (a), the black line marks Hawaiian Petrel distribution from transect surveys (Spear et al. 1995). The dashed line is a typical flight path from a satellite-tracked Maui bird during the breeding season (Adams and Flora 2009). These two regions represent the predominant areas where Hawaiian Petrels occur. In (a), the blue oval denotes an approximate area where organic matter and consumers have unusually high $\delta^{15}N$ values within the Hawaiian Petrel's range (Altabet and Francois 1994, Graham et al. 2010). In (b), the blue circle surrounding Lanai and Hawaii data points identifies petrels that apparently concentrate their foraging in a region with elevated $\delta^{15}N$. In both panels, arrows emphasize the negative relationship between latitude and $\delta^{13}C$ of marine organisms (Goericke and Fry 1994, MacKenzie et al. 2011). Hatch-year birds from Maui are outlined in red to associate them with the Maui flight path. (Reprinted with permission from Wiley et al. 2013.)

nonbreeding season, when adults apparently foraged at significantly lower latitudes.

While adult Hawaiian Petrel feather data shown in Figure 6.4 represent the early nonbreeding season, feather sampling can be designed to reflect a wide range of time frames by carefully considering molt patterns and feather growth rates. For example, sampling within a feather can yield data reflecting a period of less than 24 hours (Greylag Goose, Rohwer et al. 2015), whereas sampling multiple remiges can reflect periods separated by a full year in some albatross species that take two annual molts to replace all of their flight feathers (Edwards and Rohwer 2005). Growth bars are a visual testament to a convenient truth about feathers: moving from the oldest material at the distal tip to the most recently grown material at the proximal base, each feather represents a time series (Grubb 2006). When feathers are grown in sequence, a more extended time line is recorded in plumage, and savvy isotope researchers can choose their preferred time frame to sample within this period of feather growth, whether that be days or, in some cases, months to years. For example, in adults with sequential remige molt, isotope researchers have long recognized their ability to study foraging habits throughout the period of molt by sampling multiple primaries (Thompson and Furness 1995). More recently, Rohwer and Broms (2012) used careful attention to a combination of growth bar width and feather molt overlap to estimate molt duration. They then sampled remiges at equal time intervals for stable isotope analysis, producing a very elegant isotopic time line from museum specimens.

Isotope researchers often sample a small number of whole body contour feathers from museum specimens: this approach appeals to museum curators because it typically has little to no visual impact on a study skin and leaves many similar feathers for future studies. Body contour feathers can also generate highly useful isotope data, if the timing of their growth can be constrained. For example, in Marbled Murrelets (*Brachyramphus marmoratus*), brown-tipped breast feathers represent the pre-breeding period and all-white breast feathers represent the post-breeding period (Becker and Beissinger 2006).

However, body contour feathers are not ideal samples for species in which body contour molt is protracted or poorly characterized (e.g., many petrels; Warham 1996). In such cases, isotope data from contour feathers cannot be ascribed to a particular period of the annual cycle. It can also be difficult to know the relationship between the growth period of multiple body contour feathers, outside of qualitative observations based on relative wear. For example, if a single breast contour feather is analyzed for each individual in a study, the calendrical time periods sampled for each bird may differ. If two contour feathers are analyzed for each bird, some individuals may be represented by feathers grown simultaneously, and others by feathers grown during different days, weeks, or even months. In other words, except in cases where different body contour feather types (e.g., head versus breast) are clearly molted at different periods, it may be impossible to extend a time line beyond that represented by an individual feather. A wider variety of time periods with more precise temporal constraint can generally be accessed by sampling flight feathers in birds with sequential molt. The drawback is that remiges and rectrices are considered precious to museum study skins because they have, at most, one equivalent on any given study skin, and therefore must be sampled with great care and minimal damage.

Clearly, trade-offs are inherent in the design of museum specimen sampling strategies. Researchers may navigate these trade-offs by asking two simple questions: How can feathers be sampled so as to represent the time period of interest, and how can impact to a study skin be minimized? Generally, the best way to minimize impact to a museum skin is to take only the mass required for isotope analysis and, perhaps, for a potential backup analysis. Most isotope analyses require very small amounts of material (e.g., 1 mg), and, for many feathers, this mass can be collected with very little visual alteration (see Figure 6.5). Such a sample typically represents a few days' worth of growth, when taken from one location on one feather. If a researcher desires to study a longer period of time, a whole feather can be homogenized, or homogenization can be avoided by collecting barbs from strategic locations across one or more feathers. For example, Wiley et al. (2010) described a sampling protocol where barbs taken from near the base, middle, and tip of a feather could be combined and analyzed as a single sample that accurately represented the average $\delta^{15}N$, $\delta^{13}C$, and δD values of the entire feather (see barb sampling technique, Figure 6.5a). A similar philosophy could be used to develop minimally destructive protocols that

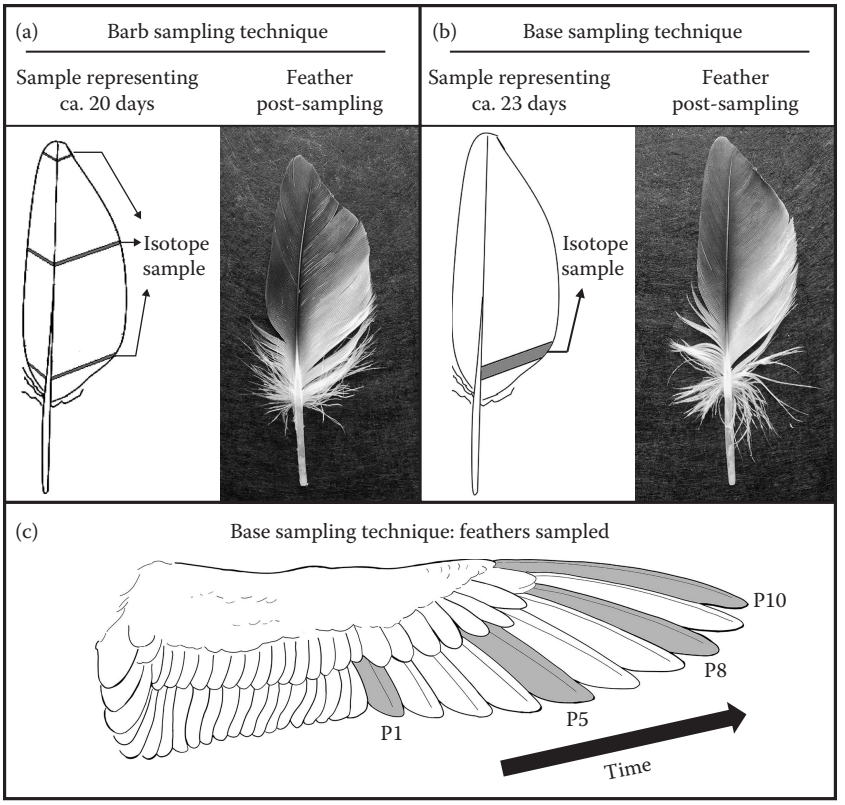

Figure 6.5. Two minimally destructive feather sampling techniques for museum study skins. (a) The barb sampling technique pictured produces isotope data reflective of the whole-feather average through strategic sampling of barbs down the length of the feather (Wiley et al. 2010). Unequal masses of barbs are taken from three locations along the feather. These subsamples are weighted so as to reflect the average distribution of mass found down the length of the feather. (b, c) The base sampling technique is less time-intensive and can easily be used for live birds. We recommend using this latter sampling technique on multiple feathers, so as to provide data from throughout the period of remige molt and data that are, together, reflective of more than very short periods of time. In (a) and (b), Hawaiian Petrel (*Pterodroma sandwichensis*) P1 is shown (length of vanes = 7 cm). Feathers are disarticulated for visualization purposes only; feathers sampled in museums and live birds are left attached to the wing. We estimated the time periods reflected by samples using growth bar width and the assumption that one growth bar is formed each day, however, we recognize the possibility that adults may form two growth bars per day, as observed in some albatross (Langston and Rohwer 1996).

represent any number of different time frames recorded in the plumage.

Alternatively, a second method of sampling remiges (Figure 6.5b,c, base sampling technique) yields isotope samples reflecting multiple, non-overlapping time periods. Here, material for a single isotope analysis is taken from the base of a primary, and multiple primaries are sampled so as to generate repeated measures from an individual bird. The resulting isotope data can be used to assess the consistency of foraging habits and the degree of individual foraging specialization throughout the period of primary molt. This protocol only compromises remiges at the base: a region that is not visible on study skins, and is difficult to access, even with manipulation. Because the bases of remiges are often white or nearly melanin-free, this protocol limits the potentially confounding effect of melanin on carbon isotope data. It is also very fast when used on a spread wing and therefore applicable to live birds. Importantly, both the protocols described in Figure 6.5 require great patience and care when used on museum specimens, especially when wings are tightly tied, but they result in little to no visible alteration of the typical study skin.

Ideal sampling strategies will depend greatly on the species of interest and the study questions.

We note that the smaller the study species, the more destructive isotope sampling protocols will be, given the convergence of minimal isotope sample mass and feather mass. However, there are many avenues through which isotope researchers can make their sampling minimally destructive, including by taking small feathers of lesser value, by sampling small, noncritical portions of feathers, or by taking very small samples from a variety of locations. We recommend that all isotope users strive for the most minimally invasive protocols possible, when sampling museum specimens. Such a practice will increase the palatability of isotope sampling requests to museum curators and preserve valuable material for future study, including increasingly sophisticated isotope research.

CHALLENGES AND RECOMMENDATIONS FOR FUTURE MUSEUM COLLECTIONS AND ISOTOPE STUDIES

Stable isotope analysis of museum specimens can clearly be used to expand our perspective of birds' phenotypes beyond the anatomy of the specimens themselves. Although traditional study skins provide valuable isotope samples, the current state of avian museum collections presents several challenges to the stable isotope researcher. First, it can be difficult to obtain sample numbers that are large enough to accurately represent a population. Stable isotope studies typically focus on aspects of ecology that are variable within a population, such as dietary tendencies. As a result, isotope users seek large sample sizes per population per time period. When a researcher wishes to study a species across its geographic range or through a series of historical time periods, to distinguish among sexes or age classes, or to leave some portion of a museum collection series untouched by destructive sampling, the problem of small sample size can be greatly compounded. Of course, this limitation applies not only to stable isotope research, but also to many types of studies in which individuals cannot be treated as equivalents (Bolnick et al. 2003).

Museums will always be limited in the number of specimens they can collect and prepare due to finite resources and concern for the health of wild bird populations. However, increased preservation of large specimen series from select populations and species would greatly increase the knowledge discernable via stable isotope research and other ecological studies. Considering the high value of archived museum specimens for isotope studies, we call on stable isotope researchers to contribute to growth of avian collections by collecting and preparing specimens themselves.

Supplemental, low-cost collections can also improve prospects for stable isotope studies. For example, the "feather files" maintained by the Bird Division of the National Museum of Natural History (Washington, DC) preserves bags of feathers that are normally discarded during preparation of skeletons. These feather collections take minutes to create and can be stored by the hundreds in the space of a single filing cabinet. More ambitiously, Smith et al. (2003) proposed widespread and systematic collection of feathers from migratory birds, to facilitate the myriad studies that use feathers as a sample medium. We agree that a concerted effort toward sampling live birds would provide a valuable complement to current, publically available avian collections. Indeed, one of the advantages of isotope-based methodology is that live birds can be sampled with limited impact by removing a feather or partial feather, taking a blood sample, or clipping a claw. If birds are not sacrificed, the same individuals can be sampled through time (within and between seasons or years), allowing researchers to construct ecological histories for individuals, and maybe even records of individuals over their entire lives. Such histories could be used to address understudied ecological topics, such as individual specialization in diet, and help to differentiate variation within versus between individuals.

In addition to curating samples, museums play a critical role in the curation of data. Pauli et al. (2015) have made a thoughtful call for large-scale archiving of stable isotope data into a so-called IsoBank, a stable isotope analog to GenBank. This endeavor could require many partners to help maintain and to organize metadata, and we encourage museums to help take a first step toward this important goal. At the very least, inclusion of isotope data from museum specimens into IsoBank would increase visibility and usefulness of these data.

Another limitation for stable isotope studies is the fact that many tissues of interest, such as muscle, liver, bone, and blood, are not commonly preserved in museum specimens, or else they are not preserved with the intention of supporting isotope studies. For example, many museums

now preserve frozen samples of soft tissue (e.g., muscle) for genetic analyses, but curators may be reluctant to use those resources to support both isotope and genetic sampling. Similarly, preparation of bird skeletons is labor-intensive, and curators are understandably reluctant to allow cutting of bone shards from these precious specimens for isotope analysis. An obvious but potentially costly solution is to increase preservation of those tissues most commonly used for isotope analysis, especially tissues with shorter turnover times that are most likely to represent the collection locality (e.g., liver) and those most amenable to retrospective studies (e.g., bone). Just as we now preserve vouchered tissues for genetic studies, we could preserve bone, muscle, and liver samples when preparing study skins. For specific projects, stable isotope researchers can collaborate with museums to collect samples during the preparation of specimens. The preparation of skeletons and study skins typically involves discarding large volumes of material that could be gleaned for isotope analysis. Isotope researchers' sampling alongside museum preparators not only takes the burden of additional curation away from museums, it allows increased flexibility to choose a range of samples on the part of the isotope researcher. Salvaging of otherwise discarded tissues is also a means of "extending" a museum specimen (Chapter 1, this volume), as it potentially increases the value of specimens through the production of associated ecological data.

Finally, we note that, although feathers are the most accessible and commonly used tissue in isotope studies involving museum specimens, feather sampling decisions can be complex, especially when knowledge of molt is incomplete. Future molt studies will clearly benefit isotope research by clarifying the time periods reflected in plumage. Isotope studies may, themselves, contribute to this knowledge of molt (Hobson et al. 2000, Neto et al. 2006). Similarly, continued study of isotope variation within the plumage of individual birds will be important to document the effects of nontarget variables (e.g., melanin concentration) on isotope data and to encourage adoption of ideal sampling strategies.

CONCLUSIONS

Stable isotope analysis is, and will continue to be, a powerful technique for the study of avian ecology and physiology. In an era of human impact on bird populations across the globe, stable isotope analysis of museum specimens may be an increasingly important means of understanding the nature and magnitude of anthropogenic change, as well as determining how best to protect dwindling bird populations. Especially when coupled with the broad taxonomic, spatial, and temporal range represented in museum collections, stable isotope analysis can increase our knowledge of changing prey bases and shifting habitat use, as well as provide information on basic dietary and migratory patterns that is essential for conservation decisions. To encourage such research outcomes, stable isotope users and museums should work toward goals of minimally destructive sampling and increased sample availability. If met, these goals will increase the material available to future generations of isotope studies, whose particular methods and questions are as yet unknown, but whose findings may be critical to our understanding of avian biology.

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