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Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean

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ABSTRACT: Stable carbon isotope signatures ($\delta^{13}C$) are increasingly being used to determine the foraging habitats of consumers in the Southern Ocean. An underlying assumption is that a latitudinal gradient in $\delta^{13}C$ values at the base of the food chain should also be reflected in organisms at higher trophic levels. Our main objective was to test that assumption by using penguin chicks (7 taxa) as predator models, because the feeding habits of provisioning adult penguins are well known during the chick-rearing period. As expected, a strong negative correlation was found between latitude and $\delta^{13}C$ values of whole blood of penguin chicks. $\delta^{13}C$ values ranged from –24.8 ± 0.5‰ in Adélie penguins living in Antarctica (67°S), to –19.5 ± 0.3‰ in northern rockhopper penguins living in the subtropics (38°S). Unlike $\delta^{13}C$ values, stable nitrogen isotope signatures ($\delta^{15}N$) were not related to latitude but instead were strongly affected by penguins' diet, with fish-eaters having higher $\delta^{15}N$ values than crustacean eaters. $\delta^{13}C$ values also reflect more local spatial foraging segregation of penguins at a subantarctic archipelago (Kerguelen Islands), where they varied from –22.3 ± 0.2‰ for king penguins feeding in oceanic waters to –15.9 ± 0.3‰ for gentoo penguins foraging in an enclosed bay. Blood $\delta^{13}C$ values moreover allowed differentiation of 2 sub-populations of gentoo penguins foraging in 2 different environments at Kerguelen. The method has 2 limitations related to the lack of longitudinal variations and to overlapping $\delta^{13}C$ values due to different isotopic gradients (latitudinal and inshore/offshore) in the marine environment. The study nevertheless shows that the $\delta^{13}C$ values of marine predators are efficient indicators of the foraging habitats at various spatial scales, both in terms of latitude in oceanic waters, and in terms of inshore/offshore gradients in waters surrounding subantarctic islands.

KEY WORDS: Antarctica · Latitude · Marine foodweb · Carbon-13 · Nitrogen-15 · Penguin · Seabird

INTRODUCTION

Establishing patterns of movements of free-ranging animals is crucial for a better understanding of their feeding ecology and life history traits, and is a prerequisite for their conservation. Tracking animal movements can be done directly using remote-sensing techniques or indirectly using biochemical markers like naturally occurring stable isotopes. The latter method has been increasingly utilized in the last decade on a variety of animals (Hobson 1999, Rubenstein & Hobson 2004), including seabirds and marine mammals (Best & Schell 1996, Cherel et al. 2000). The 2 most commonly used stable isotope ratios in ecology are those of nitrogen ($^{15}N/^{14}N$, measured as $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, $\delta^{13}C$). Consumers are typically enriched in ^{15}N relative to their food and consequently $\delta^{15}N$ measurements serve as indicators of a consumer's trophic position (McCutchan et al. 2003, Vanderklift & Ponsard 2003). By contrast, $\delta^{13}C$ values vary little along

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Table 1. Foraging characteristics of penguin species during the chick-rearing period in summer

Species	Locations	Foraging areas	Foraging range (km)	Chick diet (by mass)	Source
Southern Ocean					
Northern rockhopper penguin	Amsterdam (37.8° S)	Subtropical Zone	<10	Squid & crustaceans	Tremblay & Cherel (2003)
Southern rockhopper penguin	Crozet (46.42° S)	Polar Frontal Zone	<10	Crustaceans	Tremblay & Cherel (2003)
Macaroni penguin	Crozet (46.42° S)	Polar Frontal Zone	<50–60	Crustaceans	Barlow & Croxall (2002), Y. Cherel (unpubl. data)
King penguin	Crozet (46.42° S)	Polar Front (50° S)	340–450	Pelagic fish	Cherel & Ridoux (1992), Charrassin & Bost (2001)
	Kerguelen (49.3° S)	Polar Front (50° S)	270	Pelagic fish	Bost et al. (2002)
Emperor penguin	Adélie Land (66.7° S)	Antarctic Zone	<120	Fish	Offredo & Ridoux (1986), Rodary et al. (2000)
Adélie penguin	Adélie Land (66.7° S)	Antarctic Zone	<50	Crustaceans (fish)	Wienecke et al. (2000)
Kerguelen					
King penguin	Ratmanoff	Polar Front	270	Pelagic fish	Bost et al. (2002)
Southern rockhopper penguin	Rivière des Macaronis	Offshore	<10	Crustaceans (fish)	Tremblay & Cherel (2003), Y. Cherel (unpubl. data)
Macaroni penguin	Cap Cotter	Offshore	<50–60	Crustaceans & pelagic fish	Barlow & Croxall (2002), Y. Cherel (unpubl. data)
Gentoo penguin	Ratmanoff	Inshore (open sea)	<50	Neritic fish	Lescroël et al. (2004), Lescroël & Bost (2005)
	Morbihan Bay	Inshore (closed sea)	<15	Crustaceans	Lescroël et al. (2004), Lescroël & Bost (2005)

the food chain and are mainly used to determine primary sources in a trophic network (Kelly 2000, McCutchan et al. 2003). In the marine environment, the $\delta^{13}C$ values can also indicate inshore versus offshore, or pelagic versus benthic contribution to food intake (Hobson et al. 1994).

In comparison to higher-latitude organisms, lower-latitude plankton food bases (phytoplankton and particulate organic matter, POM) are enriched in ^{13}C. In the southern hemisphere, the geographical $\delta^{13}C$ gradient is well defined in POM from surface waters, ranging from high $\delta^{13}C$ values in warm subtropical waters in the north to low values in cold Antarctic waters in the south (François et al. 1993, Trull & Armand 2001), hence its use for the investigation of foraging areas of marine predators (Best & Schell 1996, Cherel et al. 2000, 2006). An underlying crucial assumption of these studies is that stable isotope patterns at the base of the food chain should also be reflected in organisms at higher trophic levels. The assumption has not been tested, but one recent survey of the literature on seabirds supports it (Quillfeldt et al. 2005). This review, however, suffers 2 biases. First, it is based mainly upon the carbon signature of chicks of far-ranging species of procellariiforms. During the chick-rearing period, adult procellariiforms use a dual foraging strategy including trips in different feeding areas. Chicks are fed with prey collected in different water masses and they consequently have $\delta^{13}C$ values different from those associated with foodwebs surrounding the breeding colonies (Cherel et al. 2005c). Second, Quillfeldt et al. (2005) used the isotopic values of different tissues (mainly blood and feathers). Due to different protein turnover rates and metabolic routines, those tissues are known to possess different isotopic signatures and diet-tissue isotopic discrimination factors (e.g. Hobson & Clark 1992, Cherel et al. 2005b), thus including uncontrolled and potentially confounding parameters in the analysis.

The main objective of the present study was to test the relationships between the isotopic signature of predators versus latitude in the Southern Ocean (south of the Subtropical Front). We chose penguin chicks for several practical and ecological reasons. First, our penguin colonies are located at various sites encompassing a wide latitudinal range, from the subtropical Amsterdam Island to Adélie Land, Antarctica (Table 1). We also investigated the relationship at a smaller spatial scale, within the Kerguelen Archipelago, because an extensive peri-insular shelf surrounds it, and the mainland includes a large enclosed bay where penguins are known to have different feeding habits (Lescroël & Bost 2005). The Kerguelen Archipelago thus offers a good opportunity to examine a complex inshore–offshore gradient in the marine environment. Second, a lot of information is available on the feeding habits of penguins during the chick-rearing period (Table 1). Since they do not fly and adults are central-place foragers, unlike procellariids, their foraging range is limited and most of them stay within 50 km of the colonies at that time. A notable exception is the king penguin. Whatever the locality, king penguins forage in waters of the Polar Front (Pütz 2002), and it was therefore considered to be representative of that area in summer. Finally, we used whole blood as the target tissue, because it is the easiest tissue — with feathers — that can be non-destructively sampled in the field. Blood has also the advantage that its generally low lipid content does not necessitate lipid extraction (Cherel et al. 2005b), and its isotopic signature is only marginally affected by the nutritional status of the animals (Cherel et al. 2005a).

MATERIALS AND METHODS

Fieldwork was carried out during the austral summers 2001 to 2002 and 2002 to 2003 in the Terres Australes et Antarctiques Françaises, i.e. in Adélie Land, Antarctica, and at 3 sites in the Southern Indian Ocean, the Kerguelen, Crozet and Amsterdam Islands (Table 1). According to physical oceanography, coastal Adélie Land lies in the Antarctic Zone (south of the Polar Front), Kerguelen and Crozet Archipelagoes in the Polar Frontal Zone (between the Polar Front and the Subantarctic Front) and Amsterdam Island in the Subtropical Zone (north of the Subtropical Front, i.e. slightly outside the Southern Ocean) (Park et al. 1993). Amsterdam Island is devoid of peri-insular shelf and is thus directly surrounded by oceanic waters, Crozet is a medium-sized archipelago with a relatively small shelf, but Kerguelen is the second largest archipelago in the Southern Ocean after the Falkland Islands. Its coastline is jagged by numerous fjords and bays, the largest of these bays, Morbihan Bay (located in the eastern part of the archipelago), being a very productive sheltered area where numerous seabirds, including penguins, breed.

We investigated 7 penguin taxa: 3 crested penguins (the northern *Eudyptes chrysocome moseleyi* and southern *E. chrysocome filholi* rockhopper penguins, and the macaroni penguin *E. chrysolophus*), 2 pygoscelids (the gentoo *Pygoscelis papua* and Adélie *P. adeliae* penguins) and the 2 species of the genus *Aptenodytes* (the king *A. patagonicus* and emperor *A. forsteri* penguins). For each penguin species, 8 to 11 large chicks were randomly chosen at each breeding location. Blood was collected via venipuncture of one flipper vein with heparinized syringes. Seventy-percent ethanol was then added to whole blood, because, in many cases, freezing was not possible in the field and storage in ethanol does not alter the isotopic composition of tissues (Hobson et al. 1997). Samples were subsequently kept at –20°C until isotopic analysis.

Relative abundance of stable isotopes of carbon and nitrogen in whole blood were determined by continuous-flow isotope-ratio mass spectrometry. Results are presented in the usual δ notation relative to PDB belemnite and atmospheric N_2 (Air) for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards indicate measurement errors of ± 0.1‰ and ± 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Values are means ± SD. Data were statistically analyzed using SYSTAT 9 for WINDOWS.

RESULTS

Penguin chicks from various localities segregated by their overall isotopic signatures (MANOVA, Wilk's Lambda, $F_{12,114} = 188.92$, $p < 0.0001$) and, in univariate analysis, both $\delta^{15}N$ (ANOVA, $F_{6,58} = 154.99$, $p < 0.0001$) and $\delta^{13}C$ values of whole blood ($F_{6,58} = 346.95$, $p < 0.0001$). As expected, a strong negative correlation was found between latitude and blood $\delta^{13}C$ value — but not $\delta^{15}N$ values — of penguin chicks (Spearman rank-test, n = 7, $r_s = 0.982$, $p < 0.005$) (Fig. 1). Stable carbon isotope signatures varied from –24.8 ± 0.5‰ in Adélie penguins from Adélie Land, Antarctica, to –19.5 ± 0.3‰ in northern rockhopper penguins from the subtropical Amsterdam Island. Blood $\delta^{13}C$ values differed among species with the exception of king penguins at Crozet and Kerguelen Islands, and of macaroni and southern rockhopper penguins at Crozet (post hoc Tukey HSD multiple comparison tests).

Stable nitrogen isotope values ranged from 6.8 ± 0.3‰ (southern rockhopper penguins from Crozet) to 12.4 ± 0.7‰ (emperor penguins from Adélie Land), and differed among species with the exception of the Adélie penguin and king penguins from Crozet and Kerguelen Islands (post hoc Tukey HSD multiple comparison tests) (Fig. 1).

Segregation was also found at the scale of Kerguelen Archipelago, where penguin chicks differed by their overall isotopic signatures (MANOVA, Wilk's Lambda, $F_{8,84} = 68.75$, $p < 0.0001$), and in $\delta^{15}N$ (ANOVA, $F_{4,43} = 88.24$, $p < 0.0001$) and $\delta^{13}C$ values ($F_{4,43} = 143.76$, $p < 0.0001$). Post hoc Tukey HSD multiple comparison tests indicated that all chicks differed significantly in $\delta^{15}N$ and $\delta^{13}C$ values except the macaroni and southern rockhopper penguins. When $\delta^{13}C$ values were deliberately placed in an increasing sequence, the sequence strongly reflects the known adults' foraging areas (Fig. 2). $\delta^{13}C$ values varied from –22.3 ± 0.2‰ for king penguins feeding in oceanic waters of the Polar Front

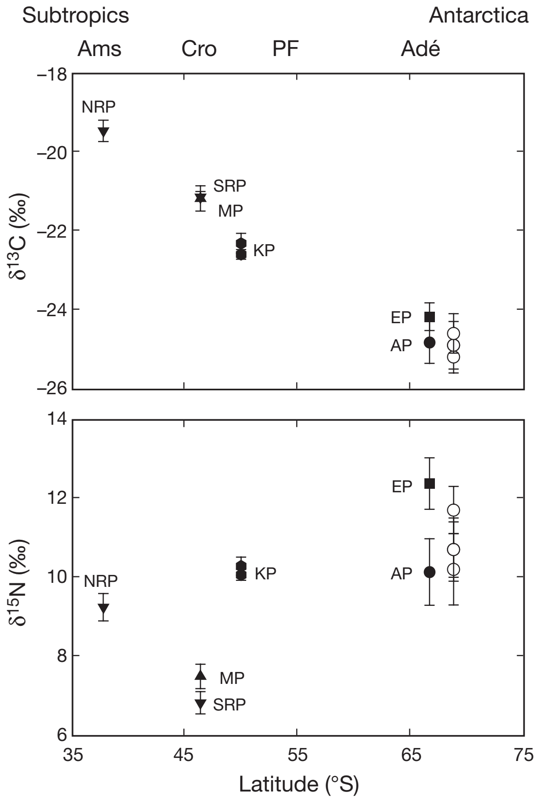

Fig. 1. Relationship between the carbon (upper panel) and nitrogen (lower panel) isotopic signatures of penguin chick blood (filled symbols) and latitude of sampling locations/foraging areas in the Southern Ocean. Open symbols refer to the blood signature of 4 species of Antarctic fulmarine petrels (Hodum & Hobson 2000). NRP: northern rockhopper penguin, SRP: southern rockhopper penguin, MP: macaroni penguin, KP: king penguin, EP: emperor penguin, AP: Adélie penguin. Ams: Amsterdam, Cro: Crozet, PF: Polar Front, Adé: Adélie Land. Values are means ± SD

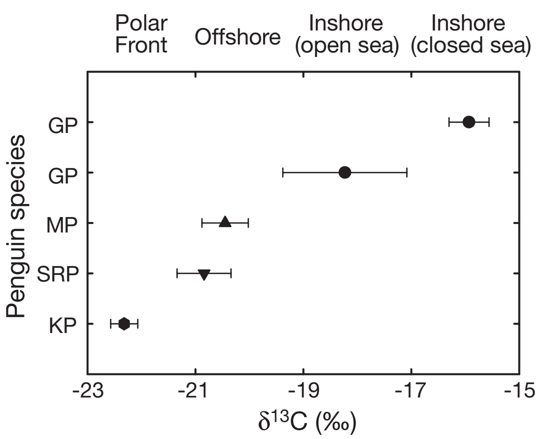

Fig. 2. Stable carbon isotope signature of penguin chick blood and adult foraging areas during the chick rearing period at Kerguelen Islands. GP: gentoo penguin, MP: macaroni penguin, SRP: southern rockhopper penguin, KP: king penguin. Values are means ± SD

to −15.9 ± 0.3‰ for gentoo penguins foraging in the enclosed Morbihan Bay, with intermediary values reached by the 2 species of offshore-forager crested penguins. Interestingly, the carbon signatures of gentoo penguin chicks whose parents fed in 2 contrasted marine environments were different, open-sea birds having lower $\delta^{13}C$ values than closed-sea penguins (Fig. 2).

DISCUSSION

Variation of penguin $\delta^{13}C$ values in the Southern Ocean

We verified the assumption that $\delta^{13}C$ patterns at the base of the food chain should be also reflected in organisms at higher trophic levels in the Southern Ocean. A strong negative correlation was found between latitude and the $\delta^{13}C$ signature of blood of top predators, with a maximum difference of 5.3‰ between the subtropical and Antarctic penguin species. The only other available data on blood $\delta^{13}C$ values of seabirds from the Southern Ocean fit well with our results (Fig. 1). The $\delta^{13}C$ signature of 4 Antarctic procellariiforms that are known to forage exclusively in Antarctic waters during breeding were indeed very negative (Hodum & Hobson 2000). Literature surveys of intermediary organisms (including penguin prey) in the trophic web of the Southern Ocean pelagic ecosystem (Quillfeldt et al. 2005) and of cephalopods worldwide (Takai et al. 2000) also showed a similar decline in $\delta^{13}C$ values with increasing latitudes in the Southern Hemisphere. However, the 2 reviews included some very negative values that are likely to be due, in part, to a lipid effect as well as differences in isotopic discrimination among different tissue types. Lipids are depleted in ^{13}C compared to proteins (Tieszen et al. 1983). Consequently, lipids must be removed from fatty tissues for a better understanding of their carbon signature, including the determination of animal feeding areas.

Results from various oceanographic cruises suggest that $\delta^{13}C$ values of surface POM in oceanic waters are not linearly related to latitudes. Instead, latitudinal changes are stepwise, with little variation in POM carbon signature within a given water mass and abrupt changes at fronts. For example, relatively constant values were observed across the Antarctic Zone with fairly steep increases across the Polar and Subantarctic Fronts (Trull & Armand 2001) and the Subtropical Front (François et al. 1993). The spatial accuracy of the determination of foraging areas of consumers using their $\delta^{13}C$ values thus operates at a large geographical scale, that of water masses and fronts (10s to 100s of km in latitude). Consequently, birds that are known to forage in the same water masses should have the same tissue $\delta^{13}C$ values. Indeed, no difference in $\delta^{13}C$ signatures was found in southern rockhopper and macaroni penguins from Crozet Islands. When breeding in sympatry, the 2 species overlapped greatly in their feeding habits, including foraging zones (Hull 1999). The importance of water masses and fronts in shaping the $\delta^{13}C$ values of oceanic consumers is also underlined by the identical $\delta^{13}C$ values of king penguins breeding at Crozet and Kerguelen Islands. An identical signature is consistent with satellite tracking showing that the 2 populations forage in the same marine environment, the Polar Front (Charrassin & Bost 2001, Bost et al. 2002). Birds from Crozet and Kerguelen, however, travel to very distinct geographical areas, thus pointing out that the method gives valuable latitudinal estimates of the foraging zones but, in contrast, $\delta^{13}C$ values gives no indication about longitude.

Unlike $\delta^{13}C$ values, $\delta^{15}N$ values of oceanic surface POM show no obvious trends with latitudes in the Southern Ocean, except a sharp increase at its northern boundary, the Subtropical Front (Altabet & François 1994, Lourey et al. 2003). Accordingly, there was no relationship between the nitrogen isotopic signature of penguin blood and latitude (Fig. 1). Since the enrichment per trophic level is striking in $\delta^{15}N$ (i.e. of the order of 3.3‰, McCutchan et al. 2003), the $\delta^{15}N$ values of penguins should be strongly affected by differences in their feeding habits and in those of their prey. Indeed, the $\delta^{15}N$ values of fish eating species (emperor and king penguins) were well above those of crustacean eaters (southern rockhopper and macaroni penguins). Dietary differences cannot, however, explain the 2.4‰ higher signature of northern than southern rockhopper penguins that forage well north and south of the Subtropical Front, respectively. The higher $\delta^{15}N$ value characterizing the base of the foodweb in warm waters is therefore the most likely explanation for that difference. It is in agreement with the elevated $\delta^{15}N$ values consistently associated with high $\delta^{13}C$ values indicating feeding in subtropical waters in oceanic seabirds (Cherel et al. 2000, 2006, Quillfeldt et al. 2005).

Variation of penguin $\delta^{13}C$ values at Kerguelen Islands

At the spatial scale of a subantarctic archipelago, the $\delta^{13}C$ values of penguins indicated the distance of their foraging areas from the coast (Fig. 2). In addition to latitudinal variations, the marine environment is characterized by benthic or inshore foodwebs that are more enriched in ^{13}C than pelagic or offshore foodwebs (France 1995). As previously described in seabird communities from the North Pacific (Hobson et al. 1994), this isotopic effect appears to integrate both a horizontal (inshore/offshore) and a vertical (benthic/pelagic) component, depending on the ultimate sources of carbon driving the foodweb. Little is known about the trophic structure of subantarctic ecosystems using stable isotopes. At the Prince Edward Islands, the 2 main types of primary producers have distinctly different $\delta^{13}C$ values, with kelp having a much more positive signature than POM, and nearshore POM being slightly enriched in ^{13}C when compared to offshore POM (Kaehler et al. 2000). The benthic/pelagic gradient thus appears much more pronounced than the inshore/offshore gradient (about 10 and 1‰, respectively). In Kerguelen penguins, the difference in $\delta^{13}C$ values amounted to 4.1‰ between open-sea gentoo penguins and the oceanic king penguins, suggesting a role of both the benthic/pelagic and the inshore/offshore gradients in shaping the penguin community. Indeed, the offshore king and crested penguins forage in the pelagic zone (Charrassin & Bost 2001, Tremblay & Cherel 2003), but open-sea gentoo penguins dive both pelagically and benthically and accordingly feed on both pelagic and benthic prey (Lescroël et al. 2004, Lescroël & Bost 2005).

At Kerguelen, the highest penguin $\delta^{13}C$ value was found in closed-sea gentoo penguins living in Morbihan Bay. This high $\delta^{13}C$ value was likely a result not only of a benthic influence, but also from high phytoplankton $\delta^{13}C$ values at the base of the pelagic foodweb because summer primary productivity is extremely elevated there (Razouls et al. 1997) and the $\delta^{13}C$ value of phytoplankton is positively linked to productivity (Laws et al. 1995). Whatever the explaining mechanisms are, however, a main point is that blood $\delta^{13}C$ values allowed us to differentiate sub-populations of the same penguin species foraging in different environments at a small spatial scale, here within the same archipelago.

Practical considerations and conclusion

In agreement with latitudinal and inshore/offshore and benthic/pelagic $\delta^{13}C$ gradients at the base of the foodweb, our study shows that the $\delta^{13}C$ signature of seabirds is an efficient tool for investigating their foraging habitats at various spatial scales. Combined with $\delta^{15}N$ analyses to help elucidate trophic effects, the method is likely applicable to other groups of consumers (Cherel & Hobson 2005) to depict the patterns of animal movements and migration. The method, however, had 2 limitations, that need careful examination in order to interpret the data correctly. First, as pointed out above, the $\delta^{13}C$ values of oceanic POM clearly show a latitudinal gradient, but there is no indication of a longitudinal one, thus explaining why some birds foraging in different areas but in identical water masses have identical $\delta^{13}C$ values. Second, latitudinal and inshore/offshore and benthic/pelagic gradients induce an overlap in the most positive $\delta^{13}C$ values of consumers, which can lead to strong misinterpretations of foraging origins. This is well illustrated in our study by comparing the blood $\delta^{13}C$ values of the subtropical northern rockhopper penguin with those of open-sea and closed-sea gentoo penguins from Kerguelen Islands. The very positive $\delta^{13}C$ values of gentoo penguins can be erroneously interpreted as birds foraging in oceanic subtropical waters (open-sea penguins) and even further north (closed-sea penguins). Consequently, a good knowledge of the biology of the studied animals, including the use of other methods, both conventional (food analysis, provisioning strategies) or not (electronic devices) are often essential to the interpretation of isotopic results and vice versa.

In the present study, the isotopic signatures of surface POM and penguin prey were not investigated. Future studies should include complementary measures to assess spatio-temporal variations of POM $\delta^{13}C$ values, their progressive integration through the foodweb, and thus their influence on the $\delta^{13}C$ values of consumers. This is essential if the stable isotopes are to be routinely used to study foraging ecology of marine predators.

Finally, a consideration inherent to the stable isotope method refers to the consistent differences in isotopic discrimination that have been found among consumer tissues (Hobson & Clark 1992, Vanderklift & Ponsard 2003). Feathers, for example, are generally more enriched in ^{15}N and ^{13}C than avian blood (Kelly 2000, Cherel et al. 2005b). Nevertheless, certain biochemical and physiological properties (protein turnover rate, metabolic routing) characterizing various tissues are similar across taxa. Consequently, comparison of isotopic signatures between individuals and taxa must be made on the same tissues to minimize inter-tissue differences.

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