REVIEW/SYNTHÈSE

Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology

Jeffrey F. Kelly

Abstract: Differential fractionation of stable isotopes of carbon during photosynthesis causes C_4 plants and C_3 plants to have distinct carbon-isotope signatures. In addition, marine C_3 plants have stable-isotope ratios of carbon that are intermediate between C_4 and terrestrial C_3 plants. The direct incorporation of the carbon-isotope ratio ($^{13}C/^{12}C$) of plants into consumers' tissues makes this ratio useful in studies of animal ecology. The heavy isotope of nitrogen (^{15}N) is preferentially incorporated into the tissues of the consumer from the diet, which results in a systematic enrichment in nitrogen-isotope ratio ($^{15}N/^{14}N$) with each trophic level. Consequently, stable isotopes of nitrogen have been used primarily to assess position in food chains. The literature pertaining to the use of stable isotopes of carbon and nitrogen in animal trophic ecology was reviewed. Data from 102 studies that reported stable-isotope ratios of carbon and (or) nitrogen of wild birds and (or) mammals were compiled and analyzed relative to diet, latitude, body size, and habitat moisture. These analyses supported the predicted relationships among trophic groups. Carbon-isotope ratios differed among species that relied on C_3, C_4, and marine food chains. Likewise, nitrogen-isotope ratios were enriched in terrestrial carnivorous mammals relative to terrestrial herbivorous mammals. Also, marine carnivores that ate vertebrates had nitrogen-isotope ratios that were enriched over the ratios of those that ate invertebrates. Data from the literature also indicated that (*i*) the carbon-isotope ratio of carnivore bone collagen was inversely related to latitude, which was likely the result of an inverse relationship between the proportion of carbon in the food chain that was fixed by C_4 plants and latitude; (*ii*) seabirds and marine mammals from northern oceans had higher nitrogen-isotope ratios than those from southern oceans; (*iii*) the nitrogen-isotope ratios of terrestrial mammals that used xeric habitats were higher than the ratios of those that used mesic habitats, indicating that water stress can have important effects on the nitrogen-isotope ratio; (*iv*) there was no relationship between body mass and nitrogen-isotope ratio for either bone collagen or muscle of carnivores; and (*v*) there was linear covariation between stable-isotope ratios of carbon and nitrogen in marine food chains (but not in terrestrial C_3 or C_4 food chains), which is likely a product of increases in carbon-isotope ratio with trophic level in marine food chains. Differences in stable-isotope composition among trophic groups were detected despite variation attributable to geographic location, climate, and analytical techniques, indicating that these effects are large and pervasive. Consequently, as knowledge of the distribution of stable isotopes of carbon and nitrogen increases, they will probably become an increasingly important tool in the study of avian and mammalian trophic ecology.

Résumé : Le fractionnement différentiel des isotopes stables de carbone durant la photosynthèse fait que les plantes C_4 et les plantes C_3 ont des signatures d'isotopes de carbone différentes. En outre, chez les plantes C_3 marines, le rapport entre les isotopes stables de carbone est intermédiaire entre celui des plantes C_4 et celui des plantes C_3 terrestres. L'intégration directe du rapport des isotopes de carbone ($^{13}C/^{12}C$) des plantes consommées dans les tissus du consommateur rend ce rapport très utile en écologie animale. L'isotope lourd de l'azote (^{15}N) est l'isotope de prédilection et il est absorbé dans les aliments pour être incorporé dans les tissus du consommateur, ce qui résulte en un enrichissement systématique du rapport entre les isotopes d'azote ($^{15}N/^{14}N$) à chaque niveau de la chaîne alimentaire. Conséquemment, des isotopes stables d'azote ont été utilisés surtout pour évaluer les positions dans la chaîne alimentaire. La littérature sur l'utilisation des isotopes stables de carbone ou d'azote en écologie animale trophique a été révisée. Les données de 102 études sur les rapports entre les isotopes stables de carbone et (ou) d'azote ont été compilées pour des oiseaux et (ou) des mammifères sauvages et examinées en fonction du régime alimentaire, de la latitude, de la taille du corps et de l'humidité dans l'habitat. Les analyses ont permis de confirmer les hypothèses sur les relations entre les groupes trophiques. Les rapports entre les isotopes de carbone diffèrent chez les espèces qui ont recours aux isotopes C_3 et C_4 ou qui se nourrissent à même la chaîne alimentaire marine. De même, les rapports entre les isotopes d'azote sont enrichis chez les mammifères carnivores terrestres par comparaison aux herbivores. De plus, chez les carnivores marins qui consomment des vertébrés, les rapports entre les isotopes d'azote sont plus élevés que chez ceux qui consomment des

Received January 28, 1999. Accepted August 10, 1999.

J.F. Kelly. Rocky Mountain Research Station, United States Department of Agriculture Forest Service, 2205 Columbia, SE Albuquerque, NM 87106, U.S.A. (e-mail: jkelly/rmrs_albq@fs.fed.us).

invertébrés. Les données de la littérature indiquent également que (*i*) le rapport entre les isotopes de carbone dans le collagène osseux des carnivores est en relation inverse avec la latitude, probablement parce q'il existe une relation inverse entre la proportion de carbone dans la chaîne alimentaire fixée par les plantes C_4 et la latitude, (*ii*) les oiseaux et les mammifères marins des mers nordiques ont des rapports entre les isotopes d'azote élevés comparativement à ceux des mers australes, (*iii*) les rapports entre les isotopes d'azote des mammifères terrestres des milieux secs sont plus élevés que ceux des mammifères de milieux mésiques, ce qui indique que le stress hydrique peut avoir des effets importants sur le rapport entre les isotopes d'azote, (*iv*) il n'y a pas de corrélation entre la masse totale et le rapport entre les isotopes d'azote, ni dans le collagène des os, ni dans les muscles des carnivores, (*v*) il y a covariation linéaire entre les rapports des isotopes de carbone et d'azote dans les chaînes alimentaires marines (mais pas dans les chaînes terrestres du C_3 ou du C_4), ce qui résulte probablement de l'augmentation des rapports entre les isotopes de carbone à mesure qu'augmente le niveau trophique. Des différences dans la composition des isotopes stables prévalent chez les différents groupes trophiques et elles sont apparentes en dépit de la variation attribuable au lieu géographique, au climat et aux techniques d'analyse, ce qui indique qu'il s'agit d'effets dominants, à grande échelle. Conséquemment, à mesure que nous acquérons des informations sur les isotopes stables de carbone et d'azote, ceux-ci sont susceptibles de devenir des outils de plus en plus importants dans l'étude de l'écologie trophique des oiseaux et des mammifères.

[Traduit par la Rédaction]

Introduction

Stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) have a broad array of applications in ecology (Peterson and Fry 1987; Rundel et al. 1989; Lajtha and Michener 1994), one of which is the investigation of the trophic ecology of wild birds and mammals. Stable isotopes of carbon and nitrogen have been used to study animal ecology since the late 1970s, and their use in studies of wild birds and mammals has grown rapidly (Fig. 1).

In the 1970s and 1980s, samples of animal tissues had to be combusted to gas (CO_2 for stable-isotope ratios of carbon and N_2 for those of nitrogen), often through a series of complex and labor-intensive procedures. After combustion, the stable-isotope ratios of the gases were measured with a dual-inlet gas isotope ratio mass spectrometer, as they are today. Because sample processing was labor-intensive and technically difficult, researchers were more limited in the number of samples they could process. This limitation on sample size probably curtailed some investigations of the subtle spatial and temporal variation that characterizes much of ecology. In 1988, a system that made it possible to obtain carbon- and nitrogen-isotope ratios from a large number of samples with minimal sample preparation became available commercially (Brand 1996). This system links a combustion furnace with a gas chromatograph interfaced with a dual-inlet gas isotope ratio mass spectrometer (Brand 1996). The important aspects of this and other advances for ecologists are that (*i*) fully automated measurement of both carbon- and nitrogen-isotope ratios from the same sample has become routine, (*ii*) the processing of up to 80 samples per day has become routine (Boutton 1991), and (*iii*) the cost of analysis has decreased.

This technical advance would be of little importance for ecologists if data on carbon- and nitrogen-isotope ratios did not provide unique information. The difficulty of getting unbiased and complete observations of foraging behavior of wild birds and mammals remains a primary problem in traditional diet studies. In many environments (e.g., fresh water, ocean, dense vegetation), it can be impossible to determine what food is being consumed through direct observation. Data obtained from both foraging observations and stomach contents have inherent biases, such as differential digestibility of prey items, that are difficult to overcome. Moreover, the complex spatial, temporal, and behavioral variation in trophic systems makes linking foraging behavior to prey populations difficult (Wiens 1984; Morrison et al. 1990; Kelly 1996). Augmenting traditional dietary information with stable-isotope data can improve understanding of the trophic ecology of birds and mammals in many instances. For these reasons, the use of stable-isotope ratios of carbon and nitrogen for understanding avian and mammalian trophic ecology has continued to grow (Fig. 1).

This review has two objectives: first, to describe what is known about the natural distributions of stable isotopes of carbon and nitrogen as they pertain to the trophic ecology of birds and mammals and, second, to use data compiled from the literature to quantify these patterns.

Units of measure and standards

The ratio of stable isotopes is expressed most often in delta (δ) notation:

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

where δ is the isotope ratio of the sample relative to a standard. R_{sample} and $R_{standard}$ are the fractions of heavy to light isotopes in the sample and standard, respectively. One is subtracted from the $R_{sample}/R_{standard}$ fraction so that samples with a lower ratio of heavy isotopes than the standard have a negative value and those with higher ratios of heavy isotopes than the standard have a positive value. This number is then multiplied by 1000 so that the δ notation is in units of parts per thousand (‰), often referred to as "per mil notation." For carbon, the international standard is the Peedee Belemnite (PDB) marine fossil limestone formation from South Carolina (Craig 1957). The standard for nitrogen is atmospheric nitrogen (Ehleringer and Rundel 1989). Most plant and animal tissues have a negative value of $\delta^{13}C$ and a positive value of $\delta^{15}N$. That is, they have a lower $^{13}C/^{12}C$ ratio than PDB and a higher $^{15}N/^{14}N$ ratio than atmospheric nitrogen.

Literature compilation and description

Stable-isotope ratios of carbon or nitrogen for wild birds or mammals were sought for statistical analysis. Key Words were used to search the BIOSIS electronic data base (1986–1997) and the Zoological Record (1993–1997). Recent stud-

Table 1. The number of species in each environment and diet category for which data on $\delta^{13}C$ and $\delta^{15}N$ values in bone collagen and muscle tissue were found.

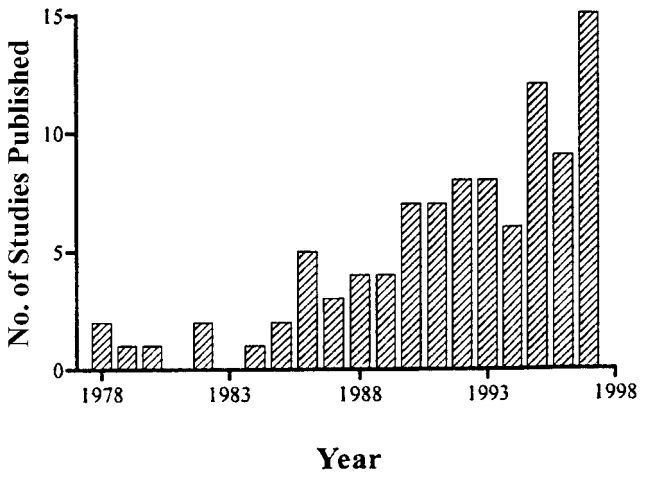
		$\delta^{13}C$ value		$\delta^{15}N$ value		$\delta^{13}C$–$\delta^{15}N$ pairs	
Environment	Diet	Bone	Muscle	Bone	Muscle	Bone	Muscle
Mammals							
Terrestrial	C_3 plant	35	4	26	3	25	0
	C_4 plant	18	2	9	0	9	0
	Invertebrate	4	3	4	0	4	0
	Vertebrate	16	1	14	1	14	0
	Omnivorous	4	0	4	0	4	0
Marine	Herbivorous	1	0	0	0	0	0
	Invertebrate	8	8	8	11	8	7
	Vertebrate	11	10	10	12	9	10
Birds							
Terrestrial	C_3 plant	2	3	1	2	1	2
	Invertebrate	1	6	1	2	1	2
	Vertebrate	3	1	3	0	3	0
Marine	Invertebrate	3	9	9	14	2	8
	Vertebrate	8	15	16	28	7	13
Grand total		114	62	105	73	87	42

ies were reviewed to generate the following keywords for the literature search: bird, mammal, stable isotope, stable carbon, stable nitrogen, carbon-13, nitrogen-15, ^{13}C, ^{15}N, $\delta^{15}N$, $\delta^{13}C$, delta^{15}N, and delta^{13}C. Because the focus of this review was wild birds and mammals, studies of rats (*Rattus rattus*) and pigs (*Sus scrofa*), which commonly were medical laboratory studies of domesticated animals, were not included. The only laboratory studies retained in the data set were those of species that occur primarily in the wild. References cited in each of these studies were reviewed to find any additional studies missed in the previous search steps. Thus, the vast majority of published studies are included. These procedures produced 102 studies of carbon- and (or) nitrogen-isotope ratios in birds and (or) mammals (Appendix, Table A1).

Of the 102 studies included in the review, 60 reported stable-isotope ratios of carbon from mammals, while 41 reported stable-isotope ratios of carbon from birds (Appendix, Table A1). Thirty-five studies reported stable-isotope ratios of nitrogen for mammals, while 32 studies reported stable-isotope ratios of nitrogen for birds. Over half the studies (53) reported values for both carbon and nitrogen. Of the 37 studies that dealt primarily with birds, 25 were concerned with a single order. Most of the 12 studies that did not concentrate on a single order dealt with seabirds. Fifty-six studies focused on mammals and 9 survey or food-web studies dealt with both birds and mammals.

Most (91) of the 102 studies reported descriptive field data and 12 reported experimental data; 3 studies reported combinations of experimental and descriptive data from the field and laboratory (Appendix, Table A1). Of the experiments, laboratory data were reported for 11 and field data for 3; the majority of studies were concerned with diet (59) or food-web structure (10). The primary concern of a surprisingly large number of studies (11) was the use of isotope data for tracking the locations of animals. Most frequently, the studies of birds (21) were done in North America. Far more studies of mammals were done in North America (26) and Africa (18) than on other continents.

Fig. 1. Histogram of the number of studies in which stable isotopes of carbon and nitrogen were used to investigate the trophic ecology of wild birds and (or) mammals.



Particularly evident was the lack of data on passerine birds and rodents. These orders are the most speciose in their respective classes, yet they provide a small fraction of the data reported. The lack of data on these groups is perhaps related to their small body size. There seems to be a clear bias toward conducting isotope research on large-bodied birds and mammals. Most data were from either terrestrial mammalian herbivores or marine carnivores. Data available from terrestrial mammals were heavily skewed toward $\delta^{13}C$ values of bone collagen, whereas data from avian and mammalian marine carnivores were slightly skewed toward $\delta^{15}N$ values of muscle (Table 1).

Delta^{13}C and $\delta^{15}N$ values for wild birds or mammals that were feeding under natural conditions were compiled from as many of these studies as possible. When more than one

measurement was available for a species, only the mean of the largest sample from a single study was used. Some analyses required only $\delta^{13}C$ or $\delta^{15}N$ values, while others required paired $\delta^{13}C$ and $\delta^{15}N$ values from the same organism. For each analysis, data from the study with the largest applicable sample size were used. That is, the $\delta^{13}C$, $\delta^{15}N$, and paired values used for a given species may each come from different studies (Appendix, Table A2).

Diets could have been classified simply by plotting the isotope data and then using a clustering algorithm to create groupings. Without a priori information on diet, however, this approach would not have provided a strong test of the ability of isotopes to distinguish among animals from different trophic groups. In contrast, using an independent data source to classify the diets of animals prior to examining the patterns in isotope ratios provides a rigorous test of the ability of stable isotopes to distinguish among trophic groups. For a priori diet classifications, Nowak (1991) and Ehrlich et al. (1988) were used for mammals and birds, respectively. Species were divided into herbivores, carnivores, and omnivores. Only species that eat both plant and animal tissues were considered omnivores. Herbivores were further categorized as eating C_3 plants or C_4 plants (C_3 plants use the enzyme Rubisco (RuBP) to fix CO_2 as part of the Calvin cycle. C_4 plants fix CO_2 with phosphoenolpyruvate (PEP) carboxylase prior to its entry into the Calvin cycle), and carnivores that eat primarily vertebrates were distinguished from those that eat primarily invertebrates. The food chain of each species was categorized as depending on C_3, C_4, or marine plants (Appendix, Table A2). Scientific names not provided in the text are included in Table A2.

The moistness of a species' habitat, the species' body size, and the latitude where the sample was collected were estimated. All estimates were obtained without reference to the isotope data. Habitat descriptions provided in the literature and in Nowak (1991) were used to categorize each terrestrial mammal's habitat as either mesic or xeric. Any species whose habitat was known to be restricted in access to permanent fresh water was categorized as mesic. For some species, no habitat description that allowed its classification as either xeric or mesic was found. For as many samples as possible, latitude was assigned on the basis of study-site descriptions. To estimate body mass, Dunning (1993) was used for birds and Silva and Downing (1995) for mammals (Appendix, Table A2).

Only analyses of bone collagen and muscle are presented, because they were the only tissues commonly reported in the literature for both birds and mammals (Table 1). Of the measurements reported on bone and muscle tissues, $\delta^{13}C$ values for bone collagen were most common, whereas $\delta^{13}C$ and $\delta^{15}N$ values for muscle tissue, particularly from terrestrial mammals, were comparatively rare. Therefore, most analyses presented compare results for bone and muscle in marine birds and mammals but only report results for bone in terrestrial mammals.

Whether lipids were extracted prior to isotope analyses was also recorded. If there was any mention of treatment with ether, chloroform, sodium hydroxide, or a Soxhlet apparatus, samples were categorized as lipid-extracted. If lipid extraction was not mentioned or implied, samples were considered to have been untreated.

Statistical analyses

When the independent variables were categorical, one-way analyses of variance (ANOVAs) were used to detect differences among categories. When ANOVAs indicated significant variation ($P < 0.05$) and there were more than two categories, least-significant-difference post-hoc tests were used. When the independent variable was continuous, linear regression analyses were employed. Residuals of all analyses were examined for heteroscedasticity, and Kolmogorov–Smirnov tests for normality were used. An α level of 0.05 was used to evaluate the significance of all tests.

Use of stable isotopes of carbon and nitrogen as dietary tracers

Carbon

History

Ehleringer and Rundel (1989) attribute the first use of stable isotopes of carbon in natural materials to Neir and Gulbransen (1939). Most natural materials have $\delta^{13}C$ values between 0 and –110‰, although most components of terrestrial, marine, and freshwater ecosystems have $\delta^{13}C$ values between 0 and –40‰ (Boutton 1991). Studies of the tissues of living organisms began in the early 1950s (Ehleringer and Rundel 1989). The first hint of the utility of carbon isotopes for the study of trophic ecology came when the difference in the isotope signatures of C_3 and C_4 plants was discovered (Bender 1971; Smith and Epstein 1971). This utility is derived from two properties: first, some sources of dietary carbon have distinct carbon-isotope signatures, and second, the isotope signature of a food is incorporated into the consumer's tissues.

Photosynthesis creates distinct carbon-isotope signatures

With regard to animal ecology, the primary process that creates sources with identifiable carbon-isotope signatures is photosynthesis. Stable isotopes of carbon are used most often to distinguish carbon fixed by terrestrial C_3 plants from that fixed by C_4 plants or marine C_3 plants. Distinguishing between C_4 plants and plants that use a third photosynthetic pathway, crassulacean acid metabolism (CAM), is difficult with carbon isotopes only, but can be done if they are used in combination with hydrogen isotopes (Sternberg 1989; Ehleringer 1991; Lajtha and Marshall 1994). Because CAM plants are relatively sparsely distributed and have not received much attention relative to animal ecology (but see Fleming et al. 1993), they are not discussed further here.

Carbon fixed by terrestrial C_3 plants ($\delta^{13}C$ = –27‰, range = –35 to –21‰) can be distinguished from that fixed by C_4 plants ($\delta^{13}C$ = –13‰, range = –14 to –10‰), because it contains relatively few ^{13}C isotopes (Boutton 1991; Ehleringer 1991). This difference is due to discrimination against ^{13}C isotopes by the primary CO_2-fixing enzyme (RuBP) of C_3 plants. In C_4 plants, the primary enzyme for CO_2 fixation (PEP carboxylase) does not discriminate against ^{13}C as strongly as that of C_3 plants (O'Leary 1981, 1988; Farquhar et al. 1989). While marine phytoplankton uses the C_3 photosynthetic pathway, its carbon-isotope signature is significantly heavier (–22‰) than that of terrestrial C_3 plants. There is some uncertainty as to the cause of this difference, but potential explanations include the use of bi-

carbonate as a carbon source in marine systems and the slower diffusion of CO_2 in water, which might counteract enzymatic discrimination (O'Leary 1988; Boutton 1991). Slow diffusion of CO_2 has been shown to cause similarly high $\delta^{13}C$ values in freshwater C_3 plants in static environments (Raven 1987). Because phytoplankton has lighter $\delta^{13}C$ values than many inshore plants (e.g., seagrasses, average $\delta^{13}C$ = –10‰, range = –15 to –3‰), inshore carbon sources can sometimes be distinguished from pelagic sources (Fry 1983; Fry and Sherr 1989; Boutton 1991; Hobson et al. 1994; Jarman et al. 1997).

Carbon-isotope ratios of consumers' tissues

Given that foods can vary considerably in their carbon-isotope signatures, the utility of these isotopes for trophic studies hinges on the relationship between the isotope composition of a consumer's diet and that of its tissues. DeNiro and Epstein (1978*a*) were the first to provide evidence that the carbon-isotope composition of a consumer was a direct reflection of its diet. They documented this pattern by feeding eight species of invertebrates and mice (*Mus musculus*) diets of known composition and then measuring the isotope composition of their tissues. DeNiro and Epstein (1978*a*) also demonstrated that whole bodies of consumers were enriched in ^{13}C only slightly over their diet (i.e., the diet–consumer fractionation of carbon isotopes was less than 2‰). Finally, they reported that the difference in the carbon-isotope values between individual tissues and diet depended on both the diet and the tissue type.

Ensuing studies have confirmed and refined these general patterns. The results of a variety of experiments have corroborated the primary conclusion that the carbon-isotope composition of birds (von Schirnding et al. 1982; Mizutani et al. 1991, 1992; Hobson and Clark 1992*a*, 1992*b*, 1993; Hobson et al. 1993; Hobson 1995) and mammals (Tieszen et al. 1983; Hobson et al. 1996; Hilderbrand et al. 1996) is a direct reflection of whether they depend on C_3, C_4, or marine food chains.

Additional studies have verified Epstein and DeNiro's (1978*a*) finding that enrichment in $\delta^{13}C$ values of whole-body samples relative to diet is slight (Haines and Montague 1979; Rau and Anderson 1981). The use of biopsy techniques, coupled with the large body size of most birds and mammals, makes whole-body samples for these taxa unusual; rather, data usually pertain to specific tissues. Experimental studies on mammals indicated that the $\delta^{13}C$ values of most tissues were within 5‰ of the diet (DeNiro and Epstein 1981; Tieszen et al. 1983; Tieszen and Boutton 1989; Hobson et al. 1996). In birds, experimental studies indicated that most tissues were enriched by 1–6‰ over the diet (e.g., Mizutani et al. 1991, 1992; Hobson and Clark 1992*b*). While enrichment of specific tissues of birds and mammals varied among studies, there were a few general patterns: (*i*) lipids tended to be highly depleted in ^{13}C, (*ii*) bone collagen and integument (skin, hair, and feathers) tended to be among the most enriched tissues in both birds and mammals, and (*iii*) there was only slight (1–2‰) enrichment of muscle tissue and whole-body samples over the diet (DeNiro and Epstein 1978*a*; Tieszen et al. 1983; Tieszen and Boutton 1989; Gearing 1991; Mizutani et al. 1991, 1992; Hobson and Clark 1992*b*; Hilderbrand et al. 1996; Hobson et al. 1996).

Field studies of mammals have indicated that bone collagen is enriched by 4–6‰ over local vegetation (e.g., van der Merwe 1982; Ambrose 1993). In these cases, however, the actual composition of the diets was unknown. In other field studies that have attempted to use $\delta^{13}C$ values to construct avian and mammalian food webs, it has been found that carbon is generally only slightly enriched (1–2‰) with each trophic step (Schoeninger and DeNiro 1984; Ambrose and DeNiro 1986; Hobson and Welch 1992; Hobson et al. 1994). Systematic enrichment in $\delta^{13}C$ values in marine food chains has been reported (Rau et al. 1983; Boutton 1991). Most studies, however, indicated that in marine environments, ^{13}C enrichment occurred at low trophic levels but not among vertebrate consumers (Rau et al. 1983; Wada et al. 1987; Fry 1988; Hobson and Welch 1992; Hobson 1993; Hobson et al. 1994).

The minor stepwise trophic enrichment of the carbon-isotope ratio that has been documented among vertebrate consumers limits its use in assessing trophic level. However, this characteristic enhances the utility of carbon-isotope ratios for tracking carbon sources through a food chain (Peterson and Fry 1987; Michener and Schell 1994). Specifically, because there is little enrichment with increase in trophic level, the carbon-isotope signature of secondary and tertiary consumers should reflect the source of carbon (C_3, C_4, or marine plants) at the base of their food chain. For example, Schoeninger and DeNiro (1984) demonstrated that for terrestrial and marine carnivores, carbon-isotope signatures were indistinguishable from those of their primary prey. Furthermore, Ambrose and DeNiro (1986) showed that among terrestrial species, carbon-isotope signatures can indicate whether carnivores had fed on herbivores that had eaten primarily C_3 or C_4 plants.

Testing trophic patterns with carbon-isotope data from field studies

The utility of $\delta^{13}C$ values for identifying the carbon sources used by consumers is most evident from the numerous field studies in which they have been used to distinguish C_3 from C_4 food chains (Teeri and Schoeller 1979; Ambrose and DeNiro 1986; Alisauskas and Hobson 1993; Fleming et al. 1993; Herrera et al. 1993; MacFadden and Cerling 1994; MacFadden 1997; Alisauskas et al. 1998) or between terrestrial (presumed C_3) and marine food chains (Schoeninger and DeNiro 1984; Hobson 1987, 1990; Mizutani et al. 1990; Hobson and Sealy 1991; Angerbjorn et al. 1994; Hilderbrand et al. 1996; Ben-David et al. 1997*a*, 1997*b*; Bearhop et al. 1999). Data compiled from such studies indicate that $\delta^{13}C$ values of bone collagen clearly distinguished between terrestrial mammalian herbivores that relied primarily on C_3 plants and those that relied primarily on C_4 plants (Table 2). Similarly, the $\delta^{13}C$ values of bone collagen varied significantly among carnivores that relied on C_4, C_3, and marine trophic chains. Bone from species that relied on C_4 food chains was enriched by 8–10‰ over bone from species that relied on C_3 food chains. The $\delta^{13}C$ values of carnivorous marine mammals were intermediate between those of C_3 and C_4 food chains; the $\delta^{13}C$ values of marine species were significantly heavier (6.3‰) than those of carnivores in C_3 food chains (Table 2). Similarly, the $\delta^{13}C$ values of marine birds were significantly enriched over those of birds from terres-

Table 2. Delta^{13}C values of birds and mammals by trophic group.

	Trophic group	Tissue	Carbon source				
			C_3	C_4	Marine	*F*	*P*
Mammals	Herbivore	Bone	–18.3±4.2	–10.1±3.8		48.9	<0.001
	Carnivore	Bone	–19.8±2.1[a]	–9.3±3.1[a]	–13.5±1.7[a]	62.6	<0.001
Birds	Carnivore	Bone	–21.3±3.9		–16.1±2.4	10.2	<0.007
	Carnivore	Muscle	–23.3±4.8		–18.8±2.2	12.0	<0.001

Note: Values are given as the mean ± SD. Sample sizes are provided in Table 1.
[a]Least-significant-difference post-hoc tests indicate that this value differs significantly from all other values in this row.

trial C_3 food chains for both bone (5.2‰) and muscle tissue (4.5‰; Table 2).

There was no significant enrichment in $\delta^{13}C$ values between mammalian herbivores and carnivores in C_3 and C_4 food chains. In fact, carnivores in C_3 food chains were, on average, depleted in ^{13}C relative to herbivores by 1.5‰ (Table 2). In C_4 trophic chains, carnivores were enriched by 0.8‰ relative to herbivores (Table 2). These slight differences support the findings of numerous studies: there is little enrichment in $\delta^{13}C$ values with increase in trophic level, at least in terrestrial mammals.

Large-scale gradients in carbon-isotope ratios

There are a number of well-known biogeographic patterns in C_3, C_4, and marine plants that create gradients in $\delta^{13}C$ values over large scales. Delta^{13}C values of C_3 terrestrial plants have been shown to be inversely correlated with latitude (Korner et al. 1991). In addition, the prevalence of C_4 plants declines with increasing latitude and altitude (Teeri and Stowe 1976; Tieszen et al. 1979). Furthermore, a latitudinal decline in $\delta^{13}C$ values has been documented in marine plankton (Sackett et al. 1965; Rau et al. 1982; Goericke et al. 1994). Some studies have shown patterns which suggest a latitudinal gradient in the $\delta^{13}C$ values of consumers' tissues and authors have speculated that this pattern might be related to the latitudinal gradients in $\delta^{13}C$ values of C_3 plants, in the proportion of C_3 to C_4 plants, and in $\delta^{13}C$ values of marine phytoplankton (Rau et al. 1982; Chamberlain et al. 1997).

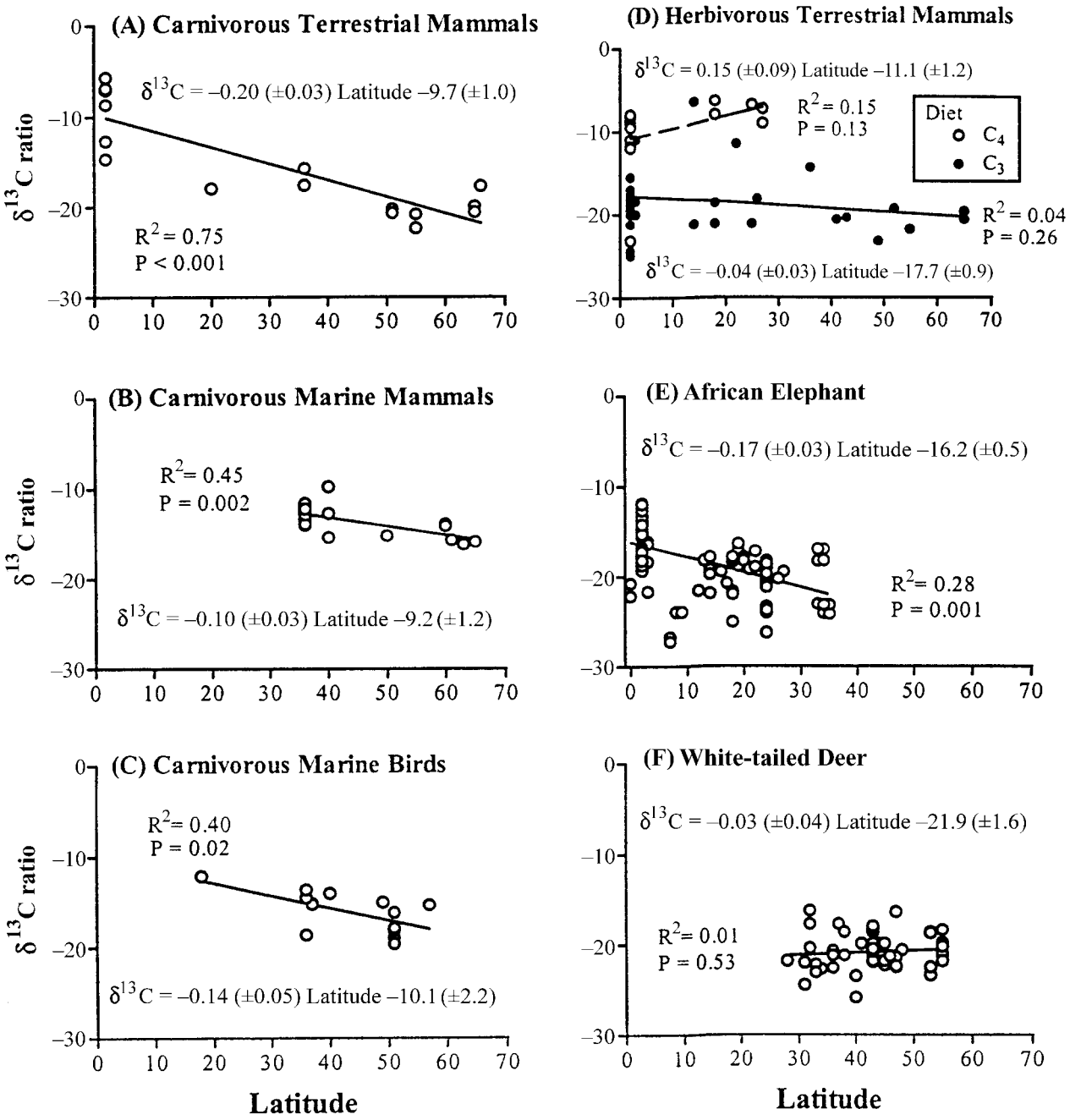
Data compiled for this review also demonstrate that $\delta^{13}C$ values of bone collagen of carnivorous marine mammals, carnivorous terrestrial mammals, and carnivorous seabirds track these latitudinal declines in $\delta^{13}C$ values (Figs. 2*a*–2*c*). Surprisingly, this pattern was not found in the bone collagen of terrestrial herbivores ($R^2 = 0.02$, $F_{[1,46]} = 1.7$, $P = 0.19$) or when the herbivores were divided into those that ate C_3 plants and those that ate C_4 plants (Fig. 2*d*). Intraspecific patterns in two herbivores for which samples were reasonably large were also examined. African elephants, *Loxodonta africana*, showed a decrease in $\delta^{13}C$ values with latitude, while there was no significant pattern among white-tailed deer, *Odocoileus virginianus* (Figs. 2*e* and 2*f*). Neither mammalian ($R^2 = 0.18$, $F_{[1,15]} = 3.3$, $P = 0.09$) nor avian ($R^2 = 0.05$, $F_{[1,22]} = 1.0$, $P = 0.32$) carnivorous marine mammals showed significant variation in $\delta^{13}C$ values of muscle tissue with latitude. Too few data were available to test for this relationship in other groups.

The latitudinal decline in $\delta^{13}C$ values of carnivorous terrestrial mammal bone is likely a direct result of similar patterns in plants at the base of the food chain. The lack of similar variation among herbivorous mammals, except African elephants, may seem to contradict the pattern in carnivores, but there is a single explanation that reconciles these patterns. Herbivorous mammals generally restrict their diet to either C_3 or C_4 plants, which is the basis of the ecological classification of browsers and grazers (see below). Within C_3 plants, the latitudinal cline in $\delta^{13}C$ values is slight relative to the distinction between C_3 and C_4 plants (Korner et al. 1991). Thus, at both the inter- and the intra-specific level, herbivorous mammals with diets restricted to C_3 plants (e.g., white-tailed deer) would be expected to show only a slight latitudinal cline in $\delta^{13}C$ values. Inter- and intra-specific patterns in those unusual herbivorous mammals that readily eat both C_3 and C_4 plants (e.g., African elephant) should, however, show relatively steep latitudinal clines. In contrast to most herbivorous mammals, carnivorous mammals are unlikely to select prey on the basis of whether they eat primarily C_3 or C_4 plants. Thus, carnivores would seem more likely than herbivores to reflect the average composition of C_3 and C_4 plants at a given locale. In this way, incorporation of prey from both C_3 and C_4 food chains in the diets of carnivores but not in the diets of herbivores may explain the latitudinal patterns evident in Fig. 2. Of course, this speculation should not be accepted without testing. In general, more research is needed to quantify the trophic linkages that maintain latitudinal gradients in $\delta^{13}C$ values. In particular, large-scale intra- and inter-specific studies that use systematic study designs to investigate the relationships between $\delta^{13}C$ values, diet, and latitude would be useful.

Effects of lipid extraction on carbon-isotope ratios

Differences in the analytical treatment of samples creates some difficulties in comparing $\delta^{13}C$ values among studies. In particular, lipids are sometimes extracted from tissues prior to stable-isotope analysis. The rationale for lipid extraction is that it is depleted in ^{13}C relative to other tissues. Lipids are most often removed with a Soxhlet apparatus, using either chloroform or ether, although sodium hydroxide has been shown to be equally effective (Ambrose 1993). The effects of lipid extraction on $\delta^{13}C$ values are greater in lipid-rich tissues (e.g., muscle, liver) than in lipid-poor tissues (e.g., hair; Tieszen and Boutton 1989). Lipids have $\delta^{13}C$ values about 6–12‰ greater than bone or muscle (DeNiro and Epstein 1977; McConnaughey and McRoy 1979; Ambrose 1990). Alexander et al. (1996) corrected for the lipid content of muscle by multiplying the percent lipid content of the tissue by the difference between the $\delta^{13}C$ values of lipid extracted and non-extracted tissues. This approach suggests

Fig. 2. Relationships between carbon-isotope ratios and latitude for carnivorous terrestrial mammals (A), carnivorous marine mammals (B), carnivorous marine birds (C), all herbivorous terrestrial mammals (D), African elephants (E), and white-tailed deer (F). The data for white-tailed deer are from Cormie and Schwarcz (1994). Equations for the regression lines are given in the form Y = slope (±SE) X + intercept (±SE). Data from north and south latitudes are pooled in A–D.



that a tissue containing 20‰ lipid would have a $\delta^{13}C$ value 2.4‰ greater when lipids were extracted than when the tissue contained lipids (0.2 × –12‰). This example is probably an extreme case, and real differences will usually be smaller (Alexander et al. 1996).

Among data compiled for this review, the use of lipid extraction appears to be idiosyncratic. For instance, lipids were extracted from nearly all muscle-tissue samples of marine birds (21 of 24), probably because muscle is a lipid-rich tissue. Lipids were extracted from half the muscle samples of marine mammals (10 of 18) and the bone samples of terrestrial herbivorous mammals (24 of 53), but from few bone samples of marine mammals (2 of 19). These data indicate that only for marine birds is there evidence of a significant difference between lipid-extracted and untreated tissues among studies (Table 3). The difference between lipid-extracted and untreated muscle (1.3‰) and bone (1.4‰) was smaller than the standard deviation for most samples (Table 3). The most powerful test was for differences in the $\delta^{13}C$ values of bone collagen among terrestrial C_3 herbivores. Interestingly, the $\delta^{13}C$ value of the lipid-extracted bone was lighter than that of untreated bone, although not

Table 3. Comparison of $\delta^{13}C$ values of tissues from which lipids were or were not extracted.

			Lipid treatment	
	Trophic group	Food chain	Extracted	Non-extracted
Muscle				
Mammals	Carnivore	Marine ns	–18.0±0.7 (10)	–18.3±0.9 (8)
		C_3	—	–18.7±1.8 (4)
	Herbivore	C_3	–28.7 (1)	–13.2±3.3 (3)
		C_4	—	–13.7±3.5 (2)
Birds	Carnivore	Marine*	–18.7±1.7 (21)	–20.0±5.2 (3)
		C_3	–18.9 (1)	–24.0±4.8 (6)
	Herbivore	C_3	–22.9±2.6 (2)	–24.4 (1)
Bone collagen				
Mammals	Carnivore	Marine ns	–16.0±0.4 (2)	–13.±1.5 (17)
		C_3 ns	–20.7±1.5 (9)	–17.1±1.2 (3)
		C_4	–9.3±3.1 (8)	—
	Herbivore	C_3 ns	–19.4±3.5 (16)	–17.3±4.8 (19)
		C_4 ns	–9.2±1.7 (8)	–10.7±4.8 (10)
	Omnivore	C_3	–19.7±1.5 (3)	–19.3 (1)
Birds	Carnivore	Marine*	–15.1±0.2 (3)	–16.5±2.7 (8)
		C_3	—	–21.3±3.9 (4)
	Herbivore	C_3	—	–21.9±0.9 (2)

Note: Values are given as the mean ± SD; numbers in parentheses are sample sizes. Differences between lipid-extracted and non-extracted values were evaluated with *t* tests when samples were adequate; ns, nonsigificant ($P > 0.05$); *, $P < 0.05$.

significantly so ($F_{[16,19]} = 3.5$, $P = 0.07$; Table 3). In fact, average values for extracted tissues were lighter than those for non-extracted tissues in most (5 of 7) groups of mammals examined (Table 3). This pattern likely indicates that for the purpose of making broad comparisons among species, lipid extraction does not create an overwhelming bias. Nonetheless, it is a systematic source of variation that may make detection of ecological patterns more difficult. Therefore, standardization of lipid-extraction techniques would undoubtedly add clarity to investigations of animal ecology that rely on isotopic tracers.

Using carbon-isotope ratios of tissues as time-integrated samples

Feeding experiments have shown that the turnover rate of isotopes in a particular tissue is a product of that tissue's metabolic rate (Tieszen et al. 1983; Hobson and Clark 1992*a*). Thus, different tissues provide dietary information that is integrated over different time scales (Hobson and Clark 1992*a*; Hilderbrand et al. 1996; Hobson et al. 1996). In Quail (*Coutrinix japonica*), for instance, blood had higher turnover rates of carbon isotopes than muscle, which in turn had higher turnover rates than bone (Hobson and Clark 1992*a*). Also, the isotope composition of hair and feathers reflects the diet at the time they were grown. This property, and that they can be sampled without killing the animal, have made these tissues particularly attractive for isotope studies (Mizutani et al. 1990, 1992; Kelly and Finch 1998; Schoeninger et al. 1997, 1998).

Carbon-isotope ratios of browsers' versus grazers' tissues

Some authors of carbon-isotope studies have divided terrestrial herbivorous mammals on the basis of whether they eat grass (grazers) or other plants (browsers) rather than whether they eat C_3 or C_4 plants. For instance, Ambrose and DeNiro (1986), DeNiro and Epstein (1978*b*), and Vogel (1978) found a clear distinction between browsers and grazers in regions of Africa where C_4 grasslands predominate, because grazers eat C_4 grasses and browsers eat C_3 forbs and shrubs. This situation is somewhat unusual in that few biomes are dominated by C_4 plants (e.g., Teeri and Stowe 1976). When grazers have access only to grasslands dominated by C_3 grasses, which is more typical, there is no difference in $\delta^{13}C$ values between browsers and grazers. For example, the grasslands of Alberta are dominated by C_3 grasses and in this environment Chisholm et al. (1986) found that the bone collagen of grazers (e.g., the bison, *Bison bison*) had $\delta^{13}C$ values between –18 and –20‰. Cormie and Schwarcz (1994) examined the bone collagen of a browser (white-tailed deer) from most regions of North America. The subset of these deer from Alberta had $\delta^{13}C$ values between –18 and –22‰. The nearly total overlap in isotope signature for bison and white-tailed deer in Alberta illustrates that with regard to isotope composition, the important distinction is whether a herbivorous mammal eats C_3 or C_4 plants and not whether it grazes or browses.

Nonetheless, for some investigations, the important ecological distinction is whether a species browses or grazes. In theory, because nearly all C_4 plants are grasses, grazers can rely on either C_3 or C_4 carbon sources, whereas browsers are confined to C_3 sources. When 54 terrestrial herbivorous mammal were classified as browsers, grazers, or mixed feeders (one species was a granivore), all 23 browsers relied on C_3 plants ($\delta^{13}C = –19.7 \pm 2.7$‰) as expected, as did 12 of 13 mixed feeders ($\delta^{13}C = –17.3 \pm 5.1$‰). Similarly 17 of 20 grazers ate C_4 plants ($\delta^{13}C = –9.7 \pm 3.0$‰). Because of a

lack of data for C_3 grazers, the practical difference between browser versus grazer and C_3 versus C_4 classification systems for data in this review is minimal.

Nitrogen

Sources with distinct nitrogen-isotope signatures

Most natural materials have $\delta^{15}N$ values between –20 and +45‰ (DeNiro and Hastorf 1985; Mizutani and Wada 1988; Mizutani et al. 1986; Peterson and Fry 1987; Ehleringer and Rundel 1989). As was the case for carbon isotopes, the utility of nitrogen isotopes in animal ecology relies on their distribution in foods and how they are incorporated into the tissues of consumers. Unlike carbon isotopes, there is no single process, like photosynthesis, that creates a large isotopic fractionation of nitrogen isotopes in plants that can be traced through food webs. Moreover, comparing $\delta^{15}N$ values across food webs or large spatial scales is problematic, particularly in terrestrial environments. The fundamental problem is that terrestrial plants vary widely in $\delta^{15}N$ values. Peterson and Fry (1987) reported foliage $\delta^{15}N$ values of between –8 and +3‰, but more positive values (up to 18‰) have been reported for desert plants (Shearer et al. 1983; Schoeninger and DeNiro 1984). This 26‰ variation (–8 to +18‰) is derived from a number of sources, primarily (*i*) the large variation in $\delta^{15}N$ values of soils ($\delta^{15}N = 9.2 \pm 2.1$‰, range = 2–12‰; Shearer et al. 1978; Shearer and Kohl 1989) and (*ii*) the systematic enrichment of deep-rooted plants over those with shallow roots (Virginia et al. 1989).

Despite this variation, it has been shown that nitrogen isotopes are useful for identifying the contributions of several types of plants to food chains. On average, $\delta^{15}N$ values of marine phytoplankton (average 7‰, range 1–16‰) tend to be enriched by about 4‰ relative to those of terrestrial plants (average 3‰, range –8 to +18‰; Schoeninger and DeNiro 1984; Sealy et al. 1987; Ambrose 1993), with the exception of plants in some marine environments where nitrogen fixation plays an important role (e.g., coral reefs and salt marshes; Capone and Carpenter 1982; Schoeninger and DeNiro 1984). Among terrestrial plants, $\delta^{15}N$ values of nitrogen-fixing plants (average 1‰, range –7 to +7‰) are depleted by 2‰, on average, relative to non-nitrogen-fixing plants (Virginia and Delwiche 1982; Schoeninger and DeNiro 1984; Virginia et al. 1989; Lajtha and Marshall 1994). This difference in nitrogen fixation in plants also has consequences for consumers. For instance, Schoeninger et al. (1998) showed that the percentage of time spent foraging on nitrogen-fixing legumes was directly related to the $\delta^{15}N$ values of white-footed sportive lemurs (*Lepilemur luecopus*). Thus, despite the large variation in $\delta^{15}N$ values of plants, there are some general patterns that can be useful for identifying sources of nitrogen in consumers' diets in special circumstances. Typically, however, it is difficult to identify the relative contribution of various plant types to food chains on the basis of nitrogen-isotope ratios.

Fractionation of nitrogen isotopes in digestion and excretion

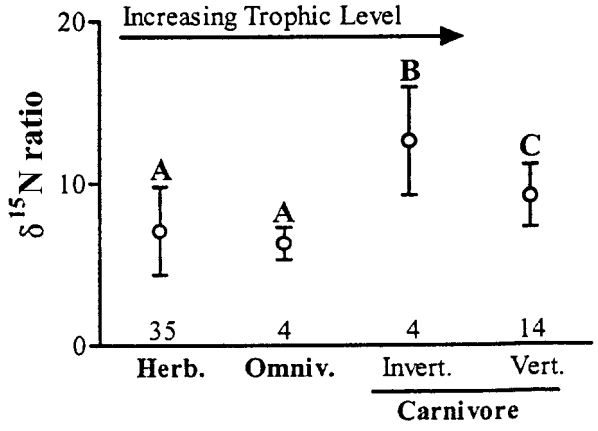
In terms of total isotope composition, the nitrogen isotopes in an animal's tissues are ultimately determined by those absorbed from the diet minus those excreted as by-products of metabolism in the form of nitrogenous wastes. The primary source of nitrogen for most animals are amino acids derived from digested proteins. In mammals at least, these amino acids enter the bloodstream and are taken up by cells, primarily in the liver or muscle, where many of them are converted to ammonia and carbohydrate through deamination or transamination. Ammonia is then converted to urea, diffused into the blood, and eventually excreted via the kidneys. Carbohydrates produced by deamination and transamination can be used to produce energy, CO_2, and water, or to build fatty acids. Most amino acids not used for energy or fat synthesis are used to build proteins (Vander et al. 1975; Eckert et al. 1988).

It is during the absorption of nitrogen isotopes from the diet and conversion of amino acids to other compounds that isotope fractionation is thought to take place (Minagwa and Wada 1984; Schoeninger and DeNiro 1984; Ambrose and DeNiro 1986). That ingested food has a higher $^{15}N/^{14}N$ ratio than feces is evidence that ^{14}N is preferentially removed from the diet in the digestive tract of mammals (Steele and Daniel 1978; Sutoh et al. 1987). Alone, this fractionation would lead to lower $\delta^{15}N$ values in the tissues of mammals than in their diets. Working in opposition to this process, however, is the fractionation of nitrogen isotopes during the production of urea or uric acid. Urea and uric acid have lower $\delta^{15}N$ values than mammalian tissues, indicating that ^{14}N is preferentially excreted (Steele and Daniel 1978; Minagwa and Wada 1984). If isotope fractionation during the absorption of nitrogen from the diet was greater than during the production of nitrogenous wastes, then $\delta^{15}N$ values in tissues of consumers would be depleted relative to the diet. In reality, the opposite is true. The fractionation associated with the production of nitrogenous waste appears to be greater than that associated with the absorption of nitrogen from the diet. That is, consumers' tissues tend to be enriched in $\delta^{15}N$ values relative to the diet rather than depleted (Minagwa and Wada 1984; Ambrose 1993; Michener and Schell 1994).

Nitrogen-isotope ratios of consumers' bodies

The primary utility of nitrogen-isotope ratios for animal ecology lies in their relationship with trophic level. DeNiro and Epstein (1981) were the first to experimentally document an average of 3‰ (range 0–10‰) enrichment in $\delta^{15}N$ values for whole-body samples over the diet. Because of limited data from whole-body samples of birds and mammals, the estimate of 3‰ enrichment of whole-body samples has not received much verification in these taxa. Studies of other taxa, however, have generally supported the 3‰ enrichment in $\delta^{15}N$ for whole bodies over diet (e.g., Minagwa and Wada 1984; Peterson and Fry 1987). Experiments that have determined the diet–tissue fractionation of nitrogen isotopes for birds and mammals show that most tissues are enriched over the diet by 1–5‰ (DeNiro and Epstein 1981; Mizutani et al. 1991, 1992; Hobson and Clark 1992*a*; Hobson et al. 1996). These studies suggest some patterns in nitrogen-isotope fractionation among tissues. Feathers, bone, and skin tend to be more enriched in ^{15}N than most tissues, and $\delta^{15}N$ values of muscle tissue more closely reflect those of the whole body than do other tissues.

Fig. 3. Nitrogen-isotope ratios (mean ± SD) of bone collagen for trophic groups of terrestrial mammals. Carnivores were divided into those that ate vertebrates and those that ate invertebrates. An ANOVA was used to test for overall significance of variation in $\delta^{15}N$ values among groups ($F_{[3,53]} = 7.8$, $P < 0.001$). Differences between specific groups were tested with least significant difference post hoc tests. Different letters denote trophic groups that differ significantly in $\delta^{15}N$ values. Numbers above the abscissa are sample sizes.



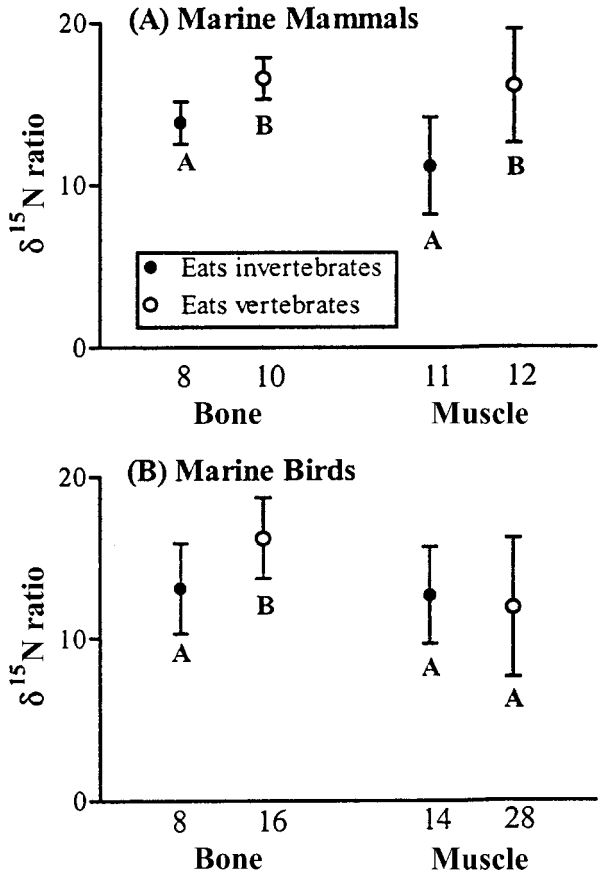
In a number of food-web studies $\delta^{15}N$ values have been successfully used to describe trophic relationships (Schoeninger and Deniro 1984; Sealy et al. 1987; Hobson and Montevecchi 1991; Rau et al. 1992; Hobson and Welch 1992; Bocherens et al. 1995; Hobson et al. 1997*c*; Kwak and Zedler 1997). In combination, these results and those of laboratory experiments support the generalization that, on average, a 3–4‰ enrichment in $\delta^{15}N$ values accompanies each trophic step (Peterson and Fry 1987; Tieszen et al. 1989; Ambrose 1993; Koch et al. 1994; Michener and Schell 1994).

Based on these patterns, herbivores are expected to have lower $\delta^{15}N$ values than carnivores. Furthermore, if trophic chains of carnivores that eat vertebrates are longer than those of carnivores that eat invertebrates, as is often implied, higher $\delta^{15}N$ values would be expected in carnivores that eat vertebrates. Finally, since omnivores, as defined for this study, eat both plants and animals, they should have $\delta^{15}N$ values intermediate between those of herbivores and carnivores. Koch et al. (1994), however, suggest that omnivores should occupy the highest trophic level.

Data from the literature indicate that $\delta^{15}N$ values of carnivores that ate invertebrates (12.6‰) were significantly enriched over herbivores, omnivores, and carnivores that ate vertebrates by 5.5, 3.4, and 5.5‰, respectively (Fig. 3). These data demonstrate that values for both groups of carnivores were significantly enriched over those for herbivores as expected. Contrary to expectations, however, carnivores that ate invertebrates had higher $\delta^{15}N$ values than those that ate vertebrates. Also at odds with predictions was the finding that omnivores had the lowest $\delta^{15}N$ values of any trophic group.

Results from marine species were more consistent with predictions. Marine mammals that ate vertebrates had significantly higher $\delta^{15}N$ values than those that ate invertebrates in both bone (2.7‰ enrichment) and muscle (4.9‰ enrichment) (Fig. 4*a*). Marine birds that ate vertebrates also had significantly higher $\delta^{15}N$ values than those that ate invertebrates in bone (3.1‰ enrichment) but not in muscle (Fig. 4*b*).

Fig. 4. Differences in nitrogen-isotope ratios (mean ± SD) of bone collagen and muscle between trophic groups of marine mammals (A) and marine birds (B). Within each tissue type, comparisons (*t* tests) were made between species that eat vertebrates and those that eat invertebrates. Samples that differ significantly are labeled with different letters. Numbers below the abscissa are sample sizes.



Seabirds and marine mammals from oceans at north-temperate and arctic latitudes had higher $\delta^{15}N$ values than those from oceans at south-temperate and antarctic latitudes. Data for all but two species of seabirds (White-tailed Tropicbird and Magnificent Frigatebird) were collected at either >30°N or >30°S. For bone and muscle, species from northern latitudes generally had greater $\delta^{15}N$ values (bone, 16.3 ± 2.1‰, $N = 19$; muscle, 14.5 ± 2.1‰, $N = 27$) than those from southern latitudes (bone, 10.9 ± 0.7‰, $N = 5$; $t = 6.4$, $P < 0.001$; muscle, 8.1 ± 3.1‰, $N = 15$; $t = 7.1$, $P < 0.001$). This pattern was also evident for mammalian muscle, where northern species had higher $\delta^{15}N$ values (14.8 ± 3.0‰, $N = 18$) than southern species (10.0 ± 5.4‰, $N = 5$; $t = 2.7$, $P < 0.02$). Only 1 of 18 bone samples of marine mammals was from a southern latitude.

The trophic-level differences between species that ate vertebrates and invertebrates were still evident when a distinction was made between northern and southern oceans. Seabirds from northern oceans that ate vertebrates had higher

Table 4. Results of an ANOVA in which the $\delta^{15}N$ value for bone collagen of terrestrial mammals was the dependent variable and trophic level (herbivore, omnivore, or carnivore) and habitat moisture (xeric or mesic) were the independent class variables; carnivores were divided into those that eat vertebrates and those that eat invertebrates.

Source of variance	Type III sum of squares	df	Mean square	*F*	*P*
Trophic level	110.2	3	36.7	7.8	<0.001
Habitat moisture	65.3	1	65.3	13.9	<0.001
Interaction	4.9	2	2.5	0.5	<0.597
Error	235.4	50	4.7		

Table 5. Delta^{15}N values of bone collagen of terrestrial mammals by trophic level; carnivores are divided into those that eat vertebrates and those that eat invertebrates.

	Habitat moisture			
Diet	Mesic	Xeric	t^a	*P*
Herbivore	6.3±2.2 (23)	8.7±2.8 (12)	2.6	0.02
Omnivore	6.3±1.0 (4)	—		
Carnivore				
Invertebrates	10.2±1.1 (2)	15.0±3.2 (2)	1.9	0.26
Vertebrates	8.2±1.9 (8)	10.6±0.7 (8)	3.4	0.01

Note: Values are given as the mean ± SD; numbers in parentheses are sample sizes.

[a]Results of *t* tests for effects within each trophic group.

$\delta^{15}N$ values (muscle: 15.4 ± 0.9‰, $N = 15$; bone: 17.2 ± 1.3‰, $N = 13$) than those that ate invertebrates (muscle: 13.2 ± 2.4‰, $N = 12$; $t = 2.9$, $P < 0.02$; bone: 14.2 ± 2.0‰, $N = 6$; $t = 3.4$, $P < 0.02$). Likewise, mammals from northern oceans that ate vertebrates had higher $\delta^{15}N$ values for muscle (16.6 ± 2.4‰, $N = 10$) than those that ate invertebrates (12.6 ± 2.1‰, $N = 8$; $t = 3.7$, $P < 0.002$). There were too few samples in some diet categories to do similar tests for species from southern oceans. In total, these results support the notion that there is a trophic-level difference between marine species that eat vertebrates and those that eat invertebrates, at least in northern oceans. The clear results obtained from marine species contrast with the complex picture for terrestrial mammals. This difference is certainly due, in part, to climatic, topographic, and edaphic influences of terrestrial environments on $\delta^{15}N$ values of plants and consumers.

Water and nutritional stress

The degree to which nitrogen isotopes are fractionated in the production of nitrogenous waste appears to be related, at least in mammals, to the water stress experienced (Ambrose and DeNiro 1986; Sealy et al. 1987; Cormie and Schwarcz 1996). The effect of water stress is thought to contribute to the finding of an inverse relationship between annual rainfall and the $\delta^{15}N$ values of consumers' tissues (Heaton et al. 1986; Sealy et al. 1987; Cormie and Schwarcz 1996). A likely explanation for this pattern is that the fractionation of nitrogen isotopes is greater in the production of concentrated nitrogenous waste than in the production of dilute nitrogenous waste, which would result in elevated $\delta^{15}N$ values (Ambrose 1991, 1993; Cormie and Schwarz 1996). The high $\delta^{15}N$ values found in plants of arid regions (Shearer et al. 1983; Heaton 1987) may also contribute to this pattern. There has been some debate about the effects of water stress on the $\delta^{15}N$ values for ruminants and hind-gut fermenters that can recycle urea to the gut as a source of nitrogen for microbial digestion. Sealy et al. (1987) have argued that this recycling of urea would result in higher $\delta^{15}N$ values in water-stressed ruminants. Ambrose (1991, 1993) argued that, without regard to recycling nitrogen, water stress alone would increase $\delta^{15}N$ values in ruminants because of increased fractionation during the production of urea. Moreover, Ambrose (1991, 1993) reasoned that in protein-stressed herbivores, the recycling of nitrogen to the gut will reduce $\delta^{15}N$ values, because the nitrogen in urea has lower $\delta^{15}N$ values than body tissues and ^{14}N is preferentially absorbed during digestion.

Nutritional stress also causes an elevation in $\delta^{15}N$ values. That is, catabolism of the body's proteins during periods of stress may elevate $\delta^{15}N$ values (Hobson and Clark 1992*b*; Ambrose 1993; Cormie and Schwarcz 1996). This pattern may help to explain the finding that $\delta^{15}N$ values can vary widely both among species fed the same diet and among individuals of the same species that are fed different diets (DeNiro and Epstein 1981). Hobson and Clark (1992*b*) showed that the fractionation factor for most tissues was greater (up to 6‰) for American Crows (*Corvus brachyramphus*) fed plant-based diets than for those fed fish (perch, *Perca flavescens*). Birds that were fed fish also gained more mass than those fed plant diets, which supports the conclusion that food stress caused these differences in fractionation between diet and tissues. This conclusion was later upheld in a combined experimental and field study that documented enriched $\delta^{15}N$ values in birds subjected to nutritional stress (Hobson et al. 1993).

Data compiled for this review demonstrate enrichment in $\delta^{15}N$ values in species that use xeric habitats relative to those that use mesic habitats. ANOVA indicated that there was an overall effect of habitat moisture on the $\delta^{15}N$ values of bone collagen for terrestrial mammals (Table 4). Even with this effect accounted for, however, the differences in $\delta^{15}N$ values among trophic levels remained significant (Table 4). For herbivores and carnivores that ate vertebrates, the use of xeric habitats was associated with significantly enriched $\delta^{15}N$ values (2.4‰) relative to species that used mesic habitats (Table 5). The few carnivores that ate invertebrates showed the same qualitative trend (4.8‰ enrichment). These values agree roughly with the few enrichment values available from controlled experiments on nutritional stress (Hobson 1993). In South Africa, an enrichment of 2.4‰ in bone collagen would be indicative of a 200-mm difference in annual rainfall (Sealy et al. 1987).

The difference in enrichment in $\delta^{15}N$ values of xeric species over mesic species was identical for herbivores and carnivores, which seems to support the urine-concentration model of Ambrose (1991, 1993) rather than the recycling model of Sealy et al. (1987). That is, if recycling of urea to the gut of herbivores is a major cause of the enrichment in $\delta^{15}N$ values in species in xeric environments, then the enrichment in herbivores should have been greater than that in carnivores, which it was not. It may also be possible, though it seems unlikely, that carnivores from xeric habitats eat nothing but herbivores from xeric habitats, which would pro-

Table 6. Results of linear regression analyses in which the $\delta^{15}N$ values of carnivores were used as the dependent variable and body mass was used as the independent variable.

	Environment	Class	Slope ($\bar{x}$ ± SE)	Intercept ($\bar{x}$ ± SE)	R^2	df	F	P_{slope}
Bone	Marine	Birds	–2.41±0.93	22.3±2.8	0.24	21	6.7	0.02
		Mammals	–0.57±0.28	18.7±1.7	0.21	16	4.2	0.06
	Terrestrial	Mammals	–0.43±0.65	11.6±2.6	0.03	16	0.4	0.52
Muscle	Marine	Birds	0.68±1.19	10.2±3.3	0.01	39	0.3	0.57
		Mammals	–1.17±0.97	20.5±5.7	0.02	21	1.5	0.24

duce an enrichment in these xeric-habitat carnivores similar to that found here. Also, since nothing is known about the protein content of the diets of the animals in the sample, Ambrose's (1991, 1993) prediction that recycling of nitrogen would lower the $\delta^{15}N$ values of protein-stressed herbivores could not be tested here. Overall, these data seem to support the notion that increased fractionation of nitrogen isotopes in the production of concentrated urine leads to elevated $\delta^{15}N$ values in species in xeric environments.

Given that $\delta^{15}N$ enrichment associated with habitat moisture is nearly as great as that associated with each trophic step, it is important for researchers to remain vigilant concerning the potential of nutritional and water stress to influence nitrogen-isotope ratios. Attempting to minimize variation due to nutritional status or climatic conditions would be worthwhile. Research aimed at determining the extent to which $\delta^{15}N$ values of consumers in arid regions are a product of (*i*) elevated ^{15}N concentrations in plants, (*ii*) increased fractionation in the production of nitrogenous wastes, or (*iii*) catabolism of body protein during periods of nutritional stress would also be useful.

Age, body size, and nitrogen-isotope ratio

Laboratory studies of nitrogen isotopes often use young animals that are still growing. Therefore, applying the results of these studies to field situations requires that isotope content and fractionation in young animals be equivalent to those of older, larger animals eating the same diet. Consequently, the relationship between body size and nitrogen-isotope ratio is of interest. A further rationale for examining the relationship between body size and $\delta^{15}N$ values is that in many taxa, body size is a determinant of diet (e.g., Werner and Gilliam 1984). Among carnivores particularly, larger species tend to occupy a higher trophic position. Thus, trophic position is, in part, dependent on body size (Peters 1983; Brown and Lomilino 1998). Relatively few studies have tested for the effects of age and body size on $\delta^{15}N$ values. They have generally looked for intraspecific patterns and, with the exception of Rau et al. (1982), found none (Minagwa and Wada 1984; Sutoh et al. 1987; Schell et al. 1989*a*, 1989*b*; Hobson and Clark 1992*b*; Best and Schell 1996). The lack of evidence for intraspecific relationships between body size and $\delta^{15}N$ values does not rule out the potential for meaningful interspecific variation, particularly since it is interspecific variation in body size that has been linked most closely to trophic position.

Data compiled for this review show no evidence of an increase in $\delta^{15}N$ values with body size. In bone collagen of seabirds, there was a significant decrease in $\delta^{15}N$ with increasing body mass (Table 6). The relationship between $\delta^{15}N$ values and body mass in marine mammals was also nearly significantly negative. These patterns are the opposite of the expected increase in $\delta^{15}N$ values with body mass. There were no patterns in the relationship between $\delta^{15}N$ values and body mass for muscle tissue of seabirds or marine mammals. The significant pattern found in bone of seabirds dissolves if the samples are divided into those from northern oceans and those from southern oceans. Thus, it seems that the difference in isotope signatures of species in northern and southern oceans is primarily responsible for the negative relationship detected between body mass and $\delta^{15}N$ values. Thus, the primary result is that there is no detectable increase in $\delta^{15}N$ values with body mass at the interspecific level, which is similar to results obtained in previous studies.

Covariation of carbon- and nitrogen-isotope ratios

There is evidence that the relative enrichment in ^{15}N in consumers' tissues is not independent of their enrichment in ^{13}C. Mizutani et al. (1991) showed a positive linear relationship between $\delta^{15}N$ and $\delta^{13}C$ values among the tissues of a single Cormorant ($\delta^{15}N = 1.11 \times \delta^{13}C + 32.3$; $R^2 = 0.85$). If there is a mechanism that links $\delta^{15}N$ and $\delta^{13}C$ values within an individual, it remains unclear. In some instances, a similar pattern has been found at the intraspecific level as well (Sealy et al. 1987; Vogel et al. 1990*a*; Cormie and Schwarz 1994; Hilderbrand et al. 1996). Sealy et al. (1987) reported a linear relationship between $\delta^{15}N$ and $\delta^{13}C$ values in humans ($\delta^{15}N = 0.57 \times \delta^{13}C + 22.5$; $R^2 = 0.19$). There is also limited evidence for linear positive associations between $\delta^{15}N$ and $\delta^{13}C$ values within food webs and across broader species assemblages (Bocherens et al. 1995; Ben-David et al. 1997*a*). Thackeray et al. (1993) reported separate relationships for African browsers ($\delta^{15}N = 1.03 \times \delta^{13}C + 28.7$; $R^2 = 0.40$) and grazers ($\delta^{15}N = –1.09 \times \delta^{13}C – 3.5$; $R^2 = 0.71$). If these relationships are purely a product of trophic-level enrichment, a slope of between 1.5 and 4 would be expected (i.e., a 3–4‰ increase in $\delta^{15}N$ values divided by a 1–2‰ increase in $\delta^{13}C$ values); all the reported relationships have slopes that are shallower than this range.

Interpretation of these relationships is difficult, particularly at the interspecific level. Data compiled for this review show a significant positive relationship between $\delta^{15}N$ and $\delta^{13}C$ values in bone collage (Fig. 5, Table 7). As is also clear from Fig. 5, however, this trend is primarily due to the relationship between the isotope signatures of C_3, C_4, and marine plants. That is, the positive relationship between $\delta^{15}N$ and $\delta^{13}C$ values in bone collage is likely the result of C_3 plants growing in more mesic areas than C_4 plants. Because $\delta^{15}N$ values are greater in species in xeric environments (Ta-

Table 7. Results of linear regression analysis in which $\delta^{15}N$ values were treated as the dependent variable and $\delta^{13}C$ values as the independent variable (significant relationships are plotted in Figs. 5 and 6).

Food chain	Tissue	Slope ($\bar{x}$ ± SE)	Intercept ($\bar{x}$ ± SE)	df	F	R^2	P_{slope}
All	Bone	0.33±0.08	15.3±1.4	85	16.8	0.16	<0.001
C_3	Bone	0.13±0.14	9.9±2.8	42	0.8	0.02	0.815
C_4	Bone	–0.07±0.31	8.9±2.9	15	0.1	0.00	0.836
$C_3 + C_4$	Bone	0.17±0.06	10.9±1.1	59	7.2	0.11	0.010
Marine	Bone	0.48±0.17	21.4±2.4	24	8.3	0.26	0.008
Marine	Muscle	1.23±0.25	37.6±4.6	36	25.0	0.41	<0.001

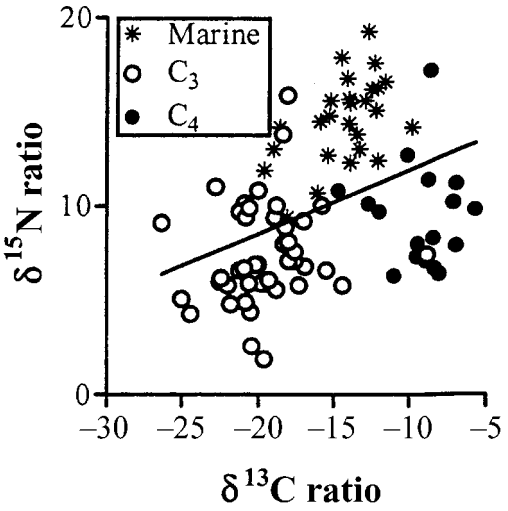
ble 5), where C_4 plants are more likely to dominate, consumers that rely on C_4 food chains will have heavier isotope ratios for both carbon and nitrogen than consumers that rely on C_3 food chains (Heaton et al. 1986; Sealy et al. 1987). This fact alone could account for the positive relationship in Fig. 4. Specifically, the 2.4‰ enrichment in $\delta^{15}N$ values in terrestrial mammals from xeric habitats over those from mesic habitats (Table 5) divided by the 8.2–10.3‰ separation between mammals dependent on C_3 versus C_4 food chains (Table 7) yields a slope of 0.23–0.29. When only data from C_3 and C_4 food chains are considered, the slope of the regression is quite close to these values (Table 7). Thus, it seems possible for a moisture gradient, from locations dominated by C_3 plants (mesic) to those dominated by C_4 plants (xeric), coupled with the difference in $\delta^{13}C$ values associated with photosynthetic pathway, to account for most of the covariation between $\delta^{15}N$ and $\delta^{13}C$ values in terrestrial mammals. It should be noted, though, that the slopes reported here are much shallower than those reported by Thackeray et al. (1993, 1996).

Within trophic systems (C_3, C_4, or marine), only consumers of marine carbon and nitrogen showed significant covariation between $\delta^{15}N$ and $\delta^{13}C$ values (Fig. 6, Table 7). The mechanism for this relationship is probably the stronger trophic enrichment in $\delta^{13}C$ values in marine environments than in terrestrial environments (Rau et al. 1983; Boutton 1991). If the trophic enrichment in carbon isotopes was 3‰, the slope would be about 1, which is within 1 SD of the actual slope for muscle tissue. In most studies, data collected for constructing food webs come from one or a few localities. It is not clear, however, how combining these data across localities influences the patterns reported here. More research is needed to explain these patterns in a quantitative fashion. This review does not support the notion that $\delta^{15}N$ and $\delta^{13}C$ values covary within C_3 and C_4 food chains. Covariation does, however, appear to be a real pattern in marine food webs. There is little quantitative understanding of how dietary patterns create covariation in $\delta^{15}N$ and $\delta^{13}C$ values at the individual, intraspecific, or interspecific level. More research on these patterns and the processes that underlie them will be required if they are to be used to gain an understanding the ecology of birds and mammals.

Summary

Despite the potential difficulties of interpreting nitrogen-isotope patterns, $\delta^{15}N$ valueshave been used successfully in a number of cases to augment traditional food-web and dietary studies and, in conjunction with $\delta^{13}C$ values, to distinguish among terrestrial, nearshore, and pelagic foraging (e.g., Hobson and Welch 1992; Hobson et al. 1994; Alexander et al. 1996; Hilderbrand et al. 1996; Ben-David et al. 1997*a*, 1997*b*; Bearhop et al. 1999). The consistent success of these studies suggests that, when attention is paid to potential pitfalls, nitrogen isotopes provide useful information about the trophic ecology of birds and mammals. For these reasons, the conclusions of this and other reviews are that (*i*) nitrogen-isotope ratios can be useful for distinguishing among diets based on marine, terrestrial, or nitrogen-fixing plants; (*ii*) nutritional and water stress can be an important source of variation in $\delta^{15}N$ values; and (*iii*) a 3–4‰ enrichment in $\delta^{15}N$ values should be expected with each trophic step (Peterson and Fry 1987; Boutton 1991; Ambrose 1993; Koch et al. 1994; Michener and Schell 1994).

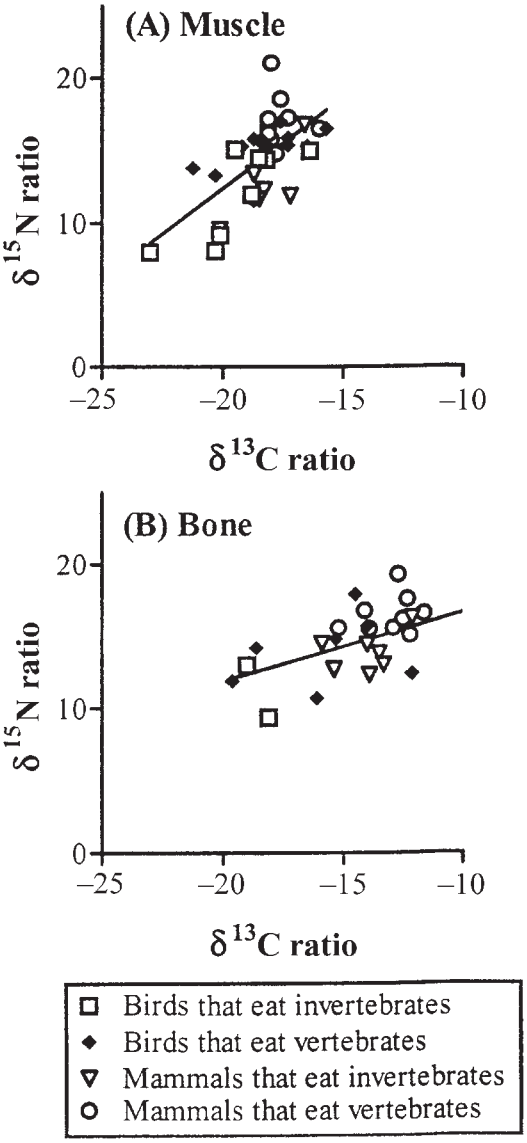
Fig. 5. Relationships between stable-isotope ratios of nitrogen and carbon in bone collagen. Species that rely on C_3, C_4, and marine food chains are indicated. The regression equation and statistics are given in Table 7.



Recommendations

The promise of using stable isotopes in studies of the ecology of birds and mammals remains vast. As is apparent from this review, much about how isotopes are distributed in plants and animals is poorly understood. Many of these limitations can be overcome with further carefully designed studies (Gannes et al. 1997). Thus, experiments, both in the laboratory and in the field, that reveal the effects of methodology (e.g., lipid extraction), physiology, and ecology on

Fig. 6. Relationships between stable-isotope ratios of nitrogen and carbon for muscle (A) and bone collagen (B) of species that rely on marine food chains. Birds and mammals are both divided into those that eat vertebrates and those that eat invertebrates. Regression equations and statistics are given in Table 7.



patterns of natural variation in stable-isotope ratios, have particular value. More direct linkages between controlled laboratory studies and descriptive field studies have the potential to increase our understanding of the trophic ecology of wild animals (Gannes et al. 1997). In addition, advances in our understanding continue to accelerate with technological advances. Because it is now possible to examine the spatial and temporal variation that is so central to ecology, studies that use stable isotopes to document this variation should be a high priority. In essence, the ideal would be to have an isotope geographic information system, that is, spatial and temporal data on isotope ratios of soil, water, plants, and animals which would provide context for further study. To this end, the potential for using museum collections to examine variation across large spatial and temporal scales would seem to be enormous (e.g., Hilderbrand et al. 1996). On another front, the potential to examine the isotope ratios of specific compounds, such as essential versus nonessential amino acids, appears to open new areas of investigation that have been heretofore untapped (Macko 1994).

A large number of the studies reviewed here report data on species that have some legal protection because they are rare. These investigations are aided by the potential to use biopsy techniques to obtain samples without jeopardizing the health of the animal; these techniques should be employed wherever possible. The use of stable-isotope techniques to aid in the conservation of these species should be lauded and supported. It has become increasingly clear that stable-isotope technology can provide information relevant to contaminant effects (Macko and Ostrom 1994; Jarman et al. 1997) and current versus historical diets (Hilderbrand et al. 1996), as well as basic trophic information that could be of value in many conservation efforts. There are numerous other applied topics where stable-isotope data could improve our ecological understanding: the effects of exotic or pest species on nutrient flows, the influences of agricultural development on habitat use, and the effects of domestic predators on urban wildlife, for instance. To expedite work on such topics, collaboration between scientists with expertise in applied conservation issues and those with a background in isotope ecology should be fostered.

Acknowledgements

Credit for what is useful in this review belongs to those who spent 20 years collecting the data presented; errors in fact or interpretation are mine. I thank I. Gilmour, K.A. Hobson, R. King, and P.T. Stapp for comments on the manuscript, V. Atudorei, J.L. Cartron, Z.D. Sharp, and T. Turner for discussions about isotope ecology, and the staff of the Rocky Mountain Research Station for support.

References

Abend, A.G., and Smith, T.D. 1995. Differences in ratios of stable isotopes of nitrogen in long-finned pilot whales (*Globicephalus melas*) in the western and eastern North Atlantic. Int. Counc. Explor. Sea J. Mar. Sci. **52**: 837–841.

Abend, A.G., and Smith, T.D. 1997. Differences in stable isotope ratios of carbon and nitrogen between long-finned pilot whales (*Globicephalus melas*) and their primary prey in the western North Atlantic. Int. Counc. Explor. Sea J. Mar. Sci. **54**: 500–503.

Alexander, S.A., Hobson, K.A., Gratto-Trevor, C.L., and Diamond, A.W. 1996. Conventional and isotopic determinations of shorebird diets at an inland stopover: the importance of invertebrates and *Potamogeton pectinatus* tubers. Can. J. Zool. **74**: 1057–1068.

Alisauskas, R.T., and Hobson, K.A. 1993. Determination of lesser snow goose diets and winter distribution using stable isotope analysis. J. Wildl. Manag. **57**: 49–54.

Alisauskas, R.T., Klaas, E.E., Hobson, K.A., and Ankney, C.D. 1998. Stable-carbon isotopes support use of adventitious color to discern winter origins of lesser snow geese. J. Field Ornithol. **69**: 262–268.

Ambrose, S.H. 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. J. Archaeol. Sci. **17**: 431–451.

Ambrose, S.H. 1991. Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial food webs. J. Archaeol. Sci. **18**: 293–317.

Ambrose, S.H. 1993. Isotopic analysis of paleodiets: methodological and interpretive considerations. *In* Investigations of ancient human tissue. *Edited by* M.K. Sanford. Gordon and Breach, Langhorne, Pa. pp. 59–130.

Ambrose, S.H., and DeNiro, M.J. 1986. The isotopic ecology of East African mammals. Oecologia, **69**: 395–406.

Ames, A.L., Van Vleet, E.S., and Sackett, W.M. 1996. The use of stable carbon analysis for determining the dietary habits of the Florida manatee, *Trichechus manatus latirostris*. Mar. Mamm. Sci. **12**: 555–563.

Angerbjorn, A., Hersteinsson, P., Liden, K., and Nelson, E. 1994. Dietary variation in Arctic foxes (*Alopex lagopus*)—an analysis of stable carbon isotopes. Oecologia, **99**: 226–232.

Bada, J.L., Peterson, R.O., Schimmelmann, A., and Hedges, R.E.M. 1990. Moose teeth as monitors of environmental isotopic parameters. Oecologia, **82**: 102–106.

Bearhop, S., Thompson, D.R., Waldron, S., Russell, I.C., Alexander, G., and Furness, R.W. 1999. Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. J. Appl. Ecol. **36**: 75–84.

Ben-David, M., Flynn, R.W., and Schell, D.M. 1997*a*. Annual changes in diets of martens: evidence from stable isotope analysis. Oecologia, **111**: 280–291.

Ben-David, M., Hanley, T.A., Klien, D.R., and Schell, D.M. 1997*b*. Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. Can. J. Zool. **75**: 803–811.

Bender, M.M. 1971. Variations in the $^{13}C/^{12}C$ ratios of plants in relation to the pathway of carbon dioxide fixation. Phytochemistry (Oxf.), **10**: 1239–1244.

Best, P.B., and Schell, D.M. 1996. Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. Mar. Biol. (Berl.), **124**: 483–494.

Bocherens, H., Fizet, M., and Mariotti, A. 1994. Diet, physiology, and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Palaeogeogr. Palaeoclimatol. Palaeoecol. **107**: 213–225.

Bocherens, H., Fogel, M.L., Tuross, N., and Zeder, M. 1995. Trophic structure and climatic information from isotopic signatures in Pleistocene cave fauna of southern England. J. Archaeol. Sci. **22**: 327–340.

Borobia, M., Gearing, P.J., Simard, Y., and Gearing, J.N. 1995. Blubber fatty acids of finback and humpback whales from the gulf of St. Lawrence. Mar. Biol. (Berl.), **122**: 341–353.

Boutton, T.W. 1991. Stable carbon isotope ratios of natural materials II: atmospheric, terrestrial, marine and freshwater environments. *In* Carbon isotope techniques. *Edited by* D.C. Coleman and B. Fry. Academic Press, San Diego. pp. 173–186.

Brand, W.A. 1996. High precision isotope ratio monitoring techniques in mass spectrometry. J. Mass Spectrom. **31**: 225–235.

Broman, D., Naf, C., Rolff, C. Zebuhr, Y., Fry, B., and Hobbie, J. 1992. Using ratios of stable nitrogen isotopes to estimate bioaccumulation and flux of polychlorinated dibenzo-*p*-dioxins (PCDDs) and dibenzofurans (PCDF) in two food chains from the North Baltic. Environ. Toxicol. Chem. **11**: 331–345.

Brown, J.N., and Lomolino, M.V. 1998. Biogeography. Sinauer Assocates Inc., Sunderland, Mass.

Capone, D.G., and Carpenter, E.J. 1982. Nitrogen fixation in the marine environment. Science (Washington, D.C.), **217**: 1140–1142.

Chamberlain, C.P., Blum, J.D., Holmes, R.T., Feng, X., Sherry, T.W., and Graves, G.R. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecologia, **109**: 132–141.

Chisholm, B., Driver, J., Dube, S., and Schwarcz, H.P. 1986. Assessment of prehistoric bison foraging and movement patterns via stable-carbon isotopic analysis. Plains Anthropol. **31**: 193–205.

Collier, K.J., and Lyon, G.L. 1991. Trophic pathways and diet of blue duck (*Hymenolaimus malacorhynchos*) on Manganuiateao River: a stable carbon isotope study. N.Z. J. Mar. Freshwater Res. **25**: 181–186.

Cormie, A.P., and Schwarcz, H.P. 1994. Stable isotopes of nitrogen and carbon of North American white-tailed deer and implications for paleodietary and other food web studies. Palaeogeogr. Palaeoclimatol. Palaeoecol. **107**: 227–241.

Cormie, A.P., and Schwarcz, H.P. 1996. Effects of climate on deer bone $\delta^{15}N$ and $\delta^{13}C$: lack of precipitation effects on $\delta^{15}N$ for animals consuming low amounts of C_4 plants. Geochim. Cosmochim. Acta, **60**: 4161–4166.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochim. Cosmochim. Acta, **12**: 133–149.

DeNiro, M.J., and Epstein, S. 1977. Mechanisms of carbon isotope fractionation associated with lipid synthesis. Science (Washington, D.C.), **197**: 261–263.

DeNiro, M.J., and Epstein, S. 1978*a*. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta, **42**: 495–506.

DeNiro, M.J., and Epstein, S. 1978*b*. Carbon isotopic evidence for different feeding patterns in two hyrax species occupying the same habitat. Science (Washington, D.C.), **210**: 906–908.

DeNiro, M.J., and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta, **45**: 341–351.

DeNiro, M.J., and Hastorf, C. 1985. Alteration of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios of plant matter during the initial stages of diagenesis: studies using archaeological specimens from Peru. Geochim Cosmochim. Acta, **49**: 97–115.

DeNiro, M.J., Schoeninger, M.J., and Hastorf, C.A. 1985. Effect of heating on the stable carbon and nitrogen isotope ratios of bone collagen. J Archaeol. Sci. **12**: 1–7.

Des Marais, D.J., Mitchell, J.M., Meinschein, W.G., and Hayes, J.M. 1980. The carbon isotope biogeochemistry of the individual hydrocarbons in bat guano and the ecology of insectivorous bats in the region of Carlsbad, New Mexico. Geochim. Cosmochim. Acta, **44**: 2075–2086.

Dunning, J.B. 1993. CRC handbook of avian body masses. CRC Press. Boca Raton, Fla.

Eckert, R., Randall, D., and Augustine, G. 1988. Animal physiology: mechanisms and adaptations. W.H. Freeman and Co., San Francisco.

Ehleringer, J.R. 1991. $^{13}C/^{12}C$ fractionation and its utility in terrestrial plant studies. *In* Carbon isotope techniques. *Edited by* D.C. Coleman and B. Fry. Academic Press, San Diego. pp. 187–201.

Ehleringer, J.R., and Rundel, P.W. 1989. Stable Isotopes: history, units, and instrumentation. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Rundel, and K.A. Nagy. Springer-Verlag, New York. pp. 1–16.

Ehrlich, P.R., Dobkin, D.S., and Wheye, D. 1988. The birders handbook. Simon and Schuster, New York.

Farquhar, G.D., Ehleringer, J.R., and Hubick, K.T. 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. **40**: 503–537.

Fleming, T.H., Nuñez, R.A., and Sternberg, L.S.L. 1993. Seasonal changes in diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. Oecologia, **94**: 72–75.

Furness, R.W., and Camphuysen, C.J. 1997. Seabirds as monitors of the marine environment. Int. Counc. Explor. Sea J. Mar Sci. **54**: 726–737.

Fry, B. 1983. Fish and shrimp migrations in the northern Gulf of Mexico analyzed using stable C, N, and S isotope ratios. Fish. Bull. **81**: 789–801.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. **33**: 1182–1190.

Fry, B., and Sherr, E.B. 1989. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Rundel, and K.A. Nagy. Springer-Verlag, New York. pp.196–229.

Gannes, L., O'Brien, D.M., and Martinez del Rio, C. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology, **78**: 1271–1276.

Gearing, J.N. 1991. The study of diet and trophic relationships through natural abundance of ^{13}C. *In* Carbon isotope techniques. *Edited by* D.C. Coleman and B. Fry. Academic Press, San Diego. pp. 201–216.

Gilmour, I., Johnston, M.A., Pillinger, C.T., Pond, C.M., Mattacks, C.A., and Prestrud, P. 1995. The carbon isotopic composition of individual fatty acids as indicators of dietary history in Arctic foxes on Svalbard. Philos. Trans. R. Soc. Lond. B Biol. Sci. **349**: 135–142.

Gloutney, M.L., and Hobson, K.A. 1998. Field preservation techniques for the analysis of stable carbon and nitrogen isotope ratios in eggs. J. Field Ornithol. **69**: 223–227.

Goericke, R., Montoya, J.P., and Fry, B. 1994. Physiology of isotopic fractionation in algae and cyanobacteria. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific, London. pp. 187–221.

Gould, P., Ostrom, P., and Walker, W. 1997. Trophic relationships of albatrosses associated with squid and large-mesh drift-net fisheries in the North Pacific Ocean. Can. J. Zool. **75**: 549–562.

Grupe, G., and Kruger, H.-H. 1990. Feeding ecology of the stone and pine marten revealed by element analysis of their skeleton. Sci. Total Environ. **90**: 227–240.

Haines, E.B., and Montague, C.L. 1979. Food sources of estuarine invertebrates analyzed using $^{13}C/^{12}C$ ratios. Ecology, **60**: 48–56.

Heaton, T.H.E. 1987. The $^{15}N/^{14}N$ ratios of plants in South Africa and Namibia: relationship to climate and coastal/saline environments. Oecologia, **74**: 236–246.

Heaton, T.H.E., Vogel, J.C., von la Chevallerie, G., and Collett, G. 1986. Climate influence on the isotopic composition of bone nitrogen. Nature (Lond.), **322**: 822–823.

Herrera, L.G., Fleming, M.T., and Findley, J.S. 1993. Geographic variation in carbon composition of the pallid bat, *Antrozous pallidus*, and its dietary implications. J. Mammal. **74**: 601–606.

Hilderbrand, G.V., Farley, S.D., Robbins, C.T., Hanley, T.A., Titus, K., and Servheen, C. 1996. Use of stable isotopes to determine diets of living and extinct bears. Can. J. Zool. **74**: 2080–2088.

Hobson, K.A. 1987. Use of stable-carbon isotope analysis to estimate marine and terrestrial protein content in gull diets. Can. J. Zool. **65**: 1210–1213.

Hobson, K.A. 1990. Stable isotope analysis of marbled murrelets: evidence for freshwater feeding and determination of trophic level. Condor, **92**: 897–903.

Hobson, K.A. 1993. Trophic relationships among high arctic seabirds: insights from tissue-dependent stable-isotope models. Mar. Ecol. Prog. Ser. **95**: 7–18.

Hobson, K.A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. Condor, **97**: 752–762.

Hobson, K.A., and Clark, R.G. 1992*a*. Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. Condor, **94**: 181–188.

Hobson, K.A., and Clark, R.G. 1992*b*. Assessing avian diets using stable isotopes II: Factors influencing diet–tissue fractionation. Condor, **94**: 189–197.

Hobson, K.A., and Clark, R.G. 1993. Turnover of ^{13}C and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. Auk, **110**: 638–641.

Hobson, K.A., and Montevecchi, W.A. 1991. Stable isotopic determinations of trophic relationships of great auks. Oecologia, **87**: 528–531.

Hobson, K.A., and Schwarcz, H.P. 1986. The variation in $\delta^{13}C$ values in bone collagen for two wild herbivore populations: implications for palaeodiet studies. J. Archaeol. Sci. **13**: 101–106.

Hobson, K.A., and Sealy, S.G. 1991. Marine protein contributions to the diet of northern saw-whet owls on the Queen Charlotte Islands: a stable-isotope approach. Auk, **108**: 437–440.

Hobson, K.A., and Sease, J.L. 1998. Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using steller sea lions. Mar. Mamm. Sci. **14**: 116–129.

Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within a high arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Prog. Ser. **84**: 9–18.

Hobson, K.A., Alisauskas, R.T., and Clark, R.G. 1993. Stable-nitrogen isotope enrichment in avian tissue due to fasting and nutritional stress: implication for isotopic analyses of diet. Condor, **95**: 388–394.

Hobson, K.A., Piatt, J.F., and Pitocchelli, J. 1994. Using stable isotopes to determine seabird trophic relationships. J. Anim. Ecol. **63**: 786–798.

Hobson, K.A., Schell, D.M., Renouf, D., and Noseworthy, E. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Can. J. Fish. Aquat. Sci. **53**: 528–533.

Hobson, K.A., Gibbs, H.L., and Gloutney, M.L. 1997*a*. Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. Can. J. Zool. **75**: 1720–1723.

Hobson, K.A., Hughes, K.D., and Ewins, P.J. 1997*b*. Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to great lakes contaminants research. Auk, **114**: 467–478.

Hobson, K.A., Sease, J.L., Merrick, R.L., and Piatt, J.F. 1997*c*. Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. Mar. Mamm. Sci. **13**: 114–132.

Horsup, A., and Marsh, H. 1992. The diet of the allied rock-wallaby, *Petrogale assimilis*, in the wet–dry tropics. Wildl. Res. **19**: 17–33.

Jarman, W.M., Hobson, K.A., Sydeman, W.J., Bacon, C.E., and McLaren, E.B. 1996. Influence of trophic position and feeding location on contaminant levels in the Gulf of the Farallones food web revealed by stable isotope analysis. Environ. Sci. Technol. **30**: 654–660.

Jarman, W.M., Sydeman, W.J., Hobson, K.A., and Bergqvist, P.-A. 1997. Relationship of polychlorinated dibenzo-*p*-dioxin and polychlorinated dibenzofuran levels to stable-nitrogen isotope

abundance in marine birds and mammals in coastal California. Environ. Toxicol. Chem. **16**: 1010–1013.

Johnson, B.J., Miller, G.H., Fogel, M.L., and Beaumont, P.B. 1997. The determination of late Quaternary paleoenvironments at Equus Cave, South Africa, using stable isotopes and amino racemization in ostrich eggshell. Palaeogeogr. Palaeoclimatol. Palaeoecol. **136**: 121–137.

Kelly, J.F. 1996. Effects of substrate on prey use by belted kingfishers (*Ceryle alcyon*): a test of the prey abundance–availability assumption. Can. J. Zool. **74**: 693–697.

Kelly, J.F., and Finch, D.M. 1998. Tracking migrant songbirds with stable isotopes. Trends Ecol. Evol. **13**: 48–49.

Koch, P.L., Fogel, M.L., and Tuross, N. 1994. Tracing the diets of fossil animals using stable isotopes. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific, London. pp. 63–92.

Koch, P.L., Heisinger, J., Moss, C., Carlson, R.W., Fogel, M.L., and Behrensmeyer, A.K. 1995. Isotopic tracking of change in diet and habitat use in African elephants. Science (Washington, D.C.), **267**: 1340–1343.

Korner, Ch., Farquhar, G.D., and Wong, S.C. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. Oecologia, **88**: 30–40.

Kwak, T.J., and Zedler, J.B. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. Oecologia, **110**: 262–277.

Lajtha, K., and Marshall, J.D. 1994. Sources of variation in the stable isotopic composition of plants. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific, London. pp. 1–21.

Lajtha, K., and Michener, R.H. 1994. Stable isotopes in ecology and environmental science. Blackwell Scientific, London.

MacFadden, B.J. 1997. Origin and evolution of the grazing guild in New World terrestrial mammals. Trends Ecol. Evol. **12**: 183–187.

MacFadden, B.J., and Cerling, T.E. 1994. Fossil horses, carbon isotopes and global change. Trends Ecol. Evol. **9**: 481–487.

Macko, S.A. 1994. Compound specific approaches using stable isotopes. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific, London. pp. 241–247.

Macko, S.A., and Ostrom, N.E. 1994. Pollution studies using stable isotopes. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific, London. pp. 45–62.

McConnaughey, T., and McRoy, C.P. 1979. Food web structure and the fractionation of carbon isotopes in the Bering Sea. Mar. Biol. (Berl.), **53**: 257–262.

McFarlane, D.A., Keeler, R.C., and Mizutani, H. 1995. Ammonia volatilization in a Mexican bat cave ecosystem. Biogeochemistry (Dordr.), **30**: 1–8.

Michener, R.H., and Schell, D.M. 1994. Stable isotope ratios as tracers in marine aquatic food webs. *In* Stable isotopes in ecology and environmental science. *Edited by* K. Lajtha and R.H. Michener. Blackwell Scientific, London. pp. 138–157.

Minagawa, M., and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta, **48**: 1135–1140.

Minami, H., Minagawa, M., and Ogi, H. 1995. Changes in stable carbon and nitrogen isotope ratios in sooty and short-tailed shearwaters during their northward migration. Condor, **97**: 565–574.

Mizutani, H., and Wada, E. 1988. Nitrogen and carbon isotope ratios in seabird rookeries and their ecological implications. Ecology, **69**: 340–349.

Mizutani, H., Kabaya, Y., and Wada, E. 1985. Ammonia volatization and high $^{15}N/^{14}N$ ratio in a penguin rookery in Antarctica. Geochem. J. **19**: 323–327.

Mizutani, H., Hasegawa, H., and Wada, E. 1986. High nitrogen isotope ratio for soils of seabird rookeries. Biogeochemistry (Dordr.), **2**: 221–247.

Mizutani, H., Fukuda, M., Kabaya, Y., and Wada, E. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. Auk, **107**: 400–437.

Mizutani, H., Kabaya, Y., and Wada, E. 1991. Nitrogen and carbon isotope compositions relate linearly in cormorant tissues and its diet. Isotopenpraxis, **27**: 166–168.

Mizutani, H., Fukuda, M., and Kabaya, Y. 1992. ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. Ecology, **73**: 1391–1395.

Moors, P.J., Speir, T.W., and Lyon, G.L. 1988. Soil analyses and $^{13}C/^{12}C$ ratios identify sites of deserted rockhopper penguin colonies. Auk, **105**: 796–799.

Morrison, M.L., Ralph, C.J., Verner, J., and Jehl, J.R., Jr. 1990. Avian foraging: theory methodology, and applications. Stud. Avian Biol. **13**: 1–515.

Muir, D.C.G., Segstro, M.D., Hobson, K.A., Ford, C.A., Stewart, R.E.A., and Olpinski, S. 1995. Can seal eating explain elevated levels of PCBs and organochlorine pesticides in walrus blubber from eastern Hudson Bay (Canada)? Environ. Pollut. **90**: 335–348.

Neir, A.O., and Gulbransen, E.A. 1939. Variations in the relative abundance of the carbon isotopes. J. Am. Chem. Soc. **61**: 697–698.

Nelson, D., Desbrosse, A., Lien, J., Ostrom, P., and Seton, R. 1991. A new stranding record of the pygmy sperm whale, *Kogia breviceps*, in waters off eastern Canada. Can. Field-Nat. **105**: 407–408.

Nowak, R.M. 1991. Walker's mammals of the world. John's Hopkins University Press, Baltimore.

O'Leary, M.H. 1981. Carbon isotope fractionations in plants. Phytochemistry (Oxf.), **20**: 553–567.

O'Leary, M.H. 1988. Carbon isotopes in photosynthesis. BioScience, **38**: 328–336.

Ostrom, P., Lein, J., and Macko, S. 1993. Evaluation of the diet of Sowerby's beaked whale, *Mesoplodon bidens*, based on isotopic comparisons among northwestern Atlantic cetaceans. Can. J. Zool. **71**: 858–861.

Peters, R.H. 1983. Ecological implications of body size. Cambridge University Press, Cambridge.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320.

Pond, C.M., Mattacks, C.A., Gilmour, I., Johnston, M.A., and Pillinger, C.T. 1995. Chemical and carbon isotopic composition of fatty acids in adipose tissue as indicators of dietary history in wild arctic foxes (*Alopex lagopus*) on Svalbard. J. Zool. (Lond.), **236**: 611–623.

Ramsay, M.A., and Hobson, K.A. 1991. Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis. Oecologia, **86**: 598–600.

Rau, G.H., and Anderson, N.H. 1981. Use of $^{13}C/^{12}C$ to trace dissolved and particulate organic matter utilization by populations of an aquatic invertebrate. Oecologia, **48**: 19–21.

Rau, G.H., Sweeney, R.E., and Kaplan, I.R. 1982. Plankton ^{13}C:^{12}C ratio changes with latitude: differences between northern and southern oceans. Deep-Sea Res. **18**: 1035–1039.

Rau, G.H., Mearns A.J., Young, D.R., Olson, R.J., Schafer, H.A., and Kaplan, I.R. 1983. Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs. Ecology, **64**: 1314–1318.

Rau, G.H., Ainley, D.G., Bengtson, J.L., Torres, J.J., and Hopkins, T.L. 1992. $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Mar. Ecol. Prog. Ser. **84**: 1–8.

Raven, J.A. 1987. Application of mass spectrometry to biochemical and physiological studies. Biochem. Plants, **13**: 127–180.

Robbins, C.T. 1983. Wildlife feeding and nutrition. Academic Press, New York.

Rundel, P.W., Ehleringer, J.R., and Nag, K.A. 1989. Stable isotopes in ecological research. Springer-Verlag, New York.

Sackett, W.M., Eckelmann, W.R., Bender, M.L., and Be, A.W.H. 1965. Temperature dependence of carbon isotope composition in marine plankton and sediments. Science (Washington, D.C.), **148**: 235–237.

Schaffner, F.C., and Swart, P.K. 1991. Influence of diet and environmental water on the carbon and oxygen isotopic signatures of seabird eggshell carbonate. Bull. Mar. Sci. **48**: 23–38.

Schell, D.M., and Ziemann, P.J. 1989. Natural carbon isotope tracers in arctic aquatic food webs. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, New York. pp. 231–251.

Schell, D.M., Saupe, S.M., and Haubenstock, N. 1989*a*. Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}C$ techniques. Mar. Biol. (Berl.), **103**: 433–443.

Schell, D.M., Saupe, S.M., and Haubenstock, N. 1989*b*. Natural isotope abundances in bowhead whale (*Balaena mysticetus*) baleen: markers of aging and habitat usage. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, New York. pp. 261–269.

Schmutz, J.A., and Hobson, K.A. 1998. Geographic, temporal and age-specific variation in diets of glaucous gulls in western Alaska. Condor, **100**: 119–130.

Schoeninger, M.J., and DeNiro, M.J. 1982. Carbon isotope ratios of apatite from fossil bone cannot be used to reconstruct diets of animals. Nature (Lond.), **297**: 1982.

Schoeninger, M.J., and DeNiro, M.J. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochim. Cosmochim. Acta, **48**: 625–639.

Schoeninger, M.J., Iwaniec, U.T., and Glander, K.E. 1997. Stable isotope ratios indicate diet and habitat use in New World monkeys. Am. J. Phys. Anthropol. **103**: 69–83.

Schoeninger, M.J., Iwaniec, U.T., and Nash, L.T. 1998. Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. Oecologia, **113**: 222–230.

Sealy, J.C., van Der Merwe, N.J., Lee Thorp, J.A., and Lanham, J.L. 1987. Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing. Geochim. Cosmochim. Acta, **51**: 2707–2717.

Shearer, G., and Kohl, D.H. 1989. Estimates of N_2 fixation in ecosystems: the need for and basis of the ^{15}N natural abundance method. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, New York. pp. 342–374.

Shearer, G., Kohl, D.H., and Virginia, R.A. 1983. Estimates of N_2-fixation from variation in the natural abundance of ^{15}N in Sonoran Desert plants. Oecologia, **56**: 365–373.

Shearer, G.B., Kohl, D.H., and Chien, S.H. 1978. The nitrogen-15 abundance in a wide variety of soils. Soil Sci. Soc. Am. J. **42**: 899–902.

Sillen, A. 1988. Elemental and isotopic analyses of mammalian fauna from southern Africa and their implications for paleodietary research. Am. J. Phys. Anthropol. **76**: 49–60.

Sillen, A., and Lee-Thorp, J.A. 1994. Trace element and isotopic aspects of predator–prey relationships in terrestrial food webs. Palaeogeogr. Palaeoclimatol. Palaeoecol. **107**: 243–255.

Silva, M., and Downing, J.A. 1995. CRC handbook of mammalian body masses. CRC Press, Boca Raton, Fla.

Smith, B.N., and Epstein, S. 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. Plant Physiol. **47**: 380–384.

Smith, R.J. Hobson, K.A., Koopman, H.N., and Lavigne, D.M. 1996. Distinguishing between populations of fresh- and salt-water harbour seals (*Phoca vitulina*) using stable-isotope ratios and fatty acid profiles. Can. J. Fish. Aquat. Sci. **53**: 272–279.

Steele, K.W., and Daniel, R.M. 1978. Fractionation of nitrogen isotopes by animals: a further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. J. Agric. Sci. **90**: 7–9.

Sternberg, L.S.L. 1989. Oxygen and hydrogen isotope ratios in plant cellulose: mechanisms and applications. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, New York. pp. 124–141.

Sukumar, R., and Ramesh, R. 1992. Stable carbon isotope ratios in Asian elephant collagen: implications for dietary studies. Oecologia, **91**: 536–539.

Sukumar, R., Bhattacharya, S.K., and Krishnamurthy, R.V. 1987. Carbon isotopic evidence for different feeding patterns in an Asian elephant population. Curr. Sci. (Bangalore), **56**: 11–14.

Sutoh, M., Koyama, T., and Yonyeyama, T. 1987. Variations of natural ^{15}N abundances in the tissues and digesta of domestic animals. Radioisotopes, **36**: 74–77.

Sydeman, W.J., Hobson, K.A., Pyle, P., and McLaren, E.B. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. Condor, **99**: 327–336.

Teeri, J.A., and Schoeller, D.A. 1979. $\delta^{13}C$ values of an herbivore and the ratio of C3 to C4 plant carbon in its diet. Oecologia, **39**: 197–200.

Teeri, J.A., and Stowe, L.G. 1976. Climatic pattern and the distribution of C_4 grasses in North America. Oecologia, **23**: 1–12.

Thackeray, J.F., van der Merwe, N.J., Lee-Thorp, J.A., and Sealy, J. 1993. Relationships between stable carbon and nitrogen isotope ratios in bone collagen of African ungulates. S. Afr. J. Zool. **89**: 458–459.

Thackeray, J.F., Henzi, S.P., and Brain, C. 1996. Stable carbon and nitrogen isotope analysis of bone collagen in *Papio cynocephalus ursinus*: comparison with ungulates and *Homo sapiens* from southern and East African environments. S. Afr. J. Sci. **92**: 209–211.

Thompson, D.R., and Furness, R.W. 1995. Stable isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern fulmars. Auk, **112**: 493–498.

Thompson, D.R., Furness, R.W., and Lewis, S.A. 1995. Diets and long-term changes in $\delta^{15}N$ and $\delta^{13}C$ values in northern fulmars, *Fulmaris glacialis*, from two northeast Atlantic colonies. Mar. Ecol. Prog. Ser. **125**: 3–11.

Tieszen, L.L., and Boutton, T.W. 1989. Stable carbon isotopes in terrestrial ecosystem research. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, New York. pp. 167–195.

Tieszen, L.L., Hein, D., Qvortrup, S., Troughton, J.N., and Imbamba, S.K. 1979. Use of $\delta^{13}C$ values to determine vegetation selectivity in east African herbivores. Oecologia, **37**: 351–359.

Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., and Slade, N.G. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia, **57**: 32–37.

Tieszen, L.L., Boutton, T.W., Ottochilo, W.K., and Nelson, D.E. 1989. An assessment of long-term food habits of Tsavo elephants based on stable carbon and nitrogen isotope ratios of bone collagen. Afr. J. Ecol. **27**: 219–226.

Vander, A.J., Sherman, J.N., and Luciano, D.S. 1975. Human physiology: the mechanisms of body function. McGraw–Hill Book Co., New York.

van der Merwe, N.J. 1982. Carbon isotopes, photosynthesis and archaeology. Am. Sci. **70**: 209–215.

van der Merwe, N.J., Lee-Thorp, J.A., and Bell, R.H.V. 1988. Carbon isotopes as indicators of elephant diets and African environments. Afr. J. Ecol. **26**: 163–172.

van der Merwe, N.J., Lee-Thorp, J.A., Thackeray, J.F., Hall-Martin, A., Krueger, F.J., Coetzee, H., Bell, R.H.V., and Lindeque, M. 1990. Source-area determination of elephant ivory by isotopic analysis. Nature (Lond.), **346**: 744–745.

Virginia, R.A., and Delwiche, C.C. 1982. Natural ^{15}N abundance of presumed N_2-fixing and non-N_2-fixing plants from selected ecosystems. Oecologia, **54**: 317–325.

Virginia, R.A., Jarrell, W.M., Rundel, P.W., Shearer, G., and Kohl, D.H. 1989. The use of variation in the natural abundance of ^{15}N to assess symbiotic nitrogen fixation by woody plants. *In* Stable isotopes in ecological research. *Edited by* P.W. Rundel, J.R. Ehleringer, and K.A. Nagy. Springer-Verlag, New York. pp. 345–394.

Vogel, J.C. 1978. Isotopic assessment of the dietary habits of ungulates. S. Afr. J. Sci. **74**: 298–301.

Vogel, J.C., Talma, A.S., Hall-Martin, A.J., and Viljoen, P.J. 1990*a*. Carbon and nitrogen isotopes in elephants. S. Afr. J. Sci. **86**: 147–150.

Vogel, J.C., Eglington, B., and Auret, J.M. 1990*b*. Isotope fingerprints in elephant bone and ivory. Nature (Lond.), **346**: 747–749.

von Schirnding, Y., van der Merwe, N.J., and Vogel, J.C. 1982. Influence of diet and age on carbon isotope ratios in ostrich eggshell. Archaeometry, **24**: 3–20.

Wada, E., Teragaki, M., Kobaya, Y., and Nemoto, T. 1987. ^{15}N and ^{13}C abundances in the Arrtic Ocean with emphasis on the biogeochemical structure of the food web. Deep-Sea Res. **34**: 829–841.

Werner, E.E., and Gilliam, J.F. 1984. the ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. **15**: 393–425.

Wiens, J.A. 1984. Resource systems, populations, and communities. *In* A new ecology. *Edited by* P.W. Price, C.N. Slobodchikoff, and W.S. Gaud. John Wiley & Sons, New York. pp. 397–436.

Appendix

Table A1. The focal taxonomic order, isotope ratios measured, the question asked, the methods used, and the continent and environment in which the study was carried out for 102 studies that report stable carbon isotope ratios and (or) stable nitrogen isotope ratios of birds and (or) mammals.

Order	Isotope[a]	Question	Methods[b]	Continent	Environment	Source
Birds						
Struthioniformes	C, N	Climate	F, D	Africa	Terrestrial	Johnson et al. 1997
	C	Diet	F, D	Africa	Terrestrial	von Schirnding et al. 1982
Sphenisciformes	C	Tracer	F, D	Australia	Marine	Moors et al. 1988
	C	Tracer	F, D	Antarctica	Marine	Mizutani et al. 1985
Procellariiformes	C, N	Food web	F, D		Marine	Gould et al. 1997
	C, N	Diet	F, D	Asia	Marine	Minami et al. 1995
	C, N	Diet	F, D	Europe	Marine	Thompson and Furness 1995
	C, N	Diet	F, D	Europe	Marine	Thompson et al. 1995
Pelecaniformes	C, N	Method	E, L	Asia	Marine	Mizutani et al. 1991
	C	Diet	F, D	Asia	Marine	Mizutani et al. 1990
Anseriiformes	C, N	Diet	B	North America	Terrestrial	Hobson et al. 1993
	C, N	Diet	F, D	North America	Terrestrial	Alisauskas and Hobson 1993
	C	Tracer	F, D	North America	Terrestrial	Alisauskas et al. 1998
	C	Diet	F, D	Australia	Terrestrial	Collier and Lyon 1991
Galliformes	C, N	Method	F, E	North America	Terrestrial	Gloutney and Hobson 1998
	C, N	Method	E, L	North America	Terrestrial	Hobson et al. 1997*a*
	C	Diet	E, L	North America	Terrestrial	Hobson and Clark 1992*a*
Charadriiformes	C, N	Diet	F, D	North America	Marine	Schmutz and Hobson 1998
	C, N	Diet	F, D	North America	Terrestrial	Alexander et al. 1996
	N	Food web	F, D	North America	Marine	Hobson and Montevecchi 1991
	C, N	Diet	F, D	North America	Marine	Hobson 1990
	C	Diet	F, D	North America	Marine	Hobson 1987
Strigiformes	C, N	Diet	F, D	North America	Terrestrial	Hobson and Sealy 1991
Passeriformes	C	Diet	E, L	North America	Terrestrial	Hobson and Clark 1993
	C	Tracer	F, D	North America	Terrestrial	Chamberlain et al. 1997
Multiple[c]	C, N	Pollution	F, D	Europe	Marine	Broman et al. 1992

Table A1 (*continued*).

	C, N	Diet	E, L	North America	Terrestrial	Hobson and Clark 1992*b*
	C, N	Diet	E, L	North America	Terrestrial	Hobson 1995
	C	Tracer	F, D	North America	Marine and terrestrial	Hobson et al. 1997*b*
	C, N	Food web	F, D	North America	Marine	Hobson et al. 1994
	C, N	Diet	F, D	North America	Marine	Kwak and Zedler 1997
	C, N	Food web	F, D	North America	Terrestrial	Hobson 1993
	C, N	Diet	E, L	Asia	Terrestrial	Mizutani et al. 1992
	C, N	Nutrient	F, D	Antarctica	Marine	Mizutani and Wada 1988
	N	Nutrient	F, D	Asia	Marine	Mizutani et al. 1986
	C	Diet	F, D	North America	Marine	Schaffner and Swart 1991
		Climate			Marine	Furness and Camphuysen 1997
Mammals						
Marsupialia	C	Diet	F, D	Australia	Terrestrial	Horsup and Marsh 1992
Chiroptera	C	Diet	F, D	North America	Terrestrial	Des Marais et al. 1980
	C	Diet	F, D	North America	Terrestrial	Fleming et al. 1993
	N	Nutrient	F, D	North America	Terrestrial	McFarlane et al. 1995
	C	Diet	F, D	North America	Terrestrial	Herrera et al. 1993
Primates	C, N	Diet	F, D	South America	Terrestrial	Schoeninger et al. 1997
	C, N	Diet	F, D	Africa	Terrestrial	Schoeninger et al. 1998
	C, N	Paleontology	F, D	Africa	Terrestrial	Thackeray et al. 1996
Cetacea	N	Tracer	F, D	Europe	Marine	Abend and Smith 1995
	N	Diet	F, D	North America	Marine	Abend and Smith 1997
	C	Tracer	F, D	Africa	Marine	Best and Schell 1996
	C	Diet	F, D	North America	Marine	Borobia et al. 1995
	C, N	Diet	F, D	North America	Marine	Nelson et al. 1991
	C, N	Diet	F, D	North America	Marine	Ostrom et al. 1993
	C	Tracer	F, D	North America	Marine	Schell et al. 1989*a*
	C	Tracer	F, D	North America	Marine	Schell et al. 1989*b*
Carnivora	C, N	Diet	F, D	North America	Terrestrial	Ben-David et al. 1997*a*
	C, N	Diet	F, D	North America	Terrestrial	Ben-David et al. 1997*b*
	C	Diet	F, D	Europe	Terrestrial	Angerbjorn et al. 1994
	C	Diet	F, D	Europe	Terrestrial	Gilmour et al. 1995
	C	Diet	F, D	Europe	Terrestrial	Grupe and Krueger 1990
	C, N	Diet	B	North America	Terrestrial	Hilderbrand et al. 1996
	C	Diet	F, D	Europe	Terrestrial	Pond et al. 1995
	C	Diet	F, D	North America	Terrestrial	Ramsay and Hobson 1991
	C	Food web	F, D	Africa	Terrestrial	Sillen and Lee-Thorp 1994
Pinnipedia	C, N	Diet	F, D	North America	Marine	Hobson and Sease 1998
	C, N	Food web	F, D	North America	Marine	Hobson et al. 1997*c*
	C, N	Diet	E, L	North America	Marine	Hobson et al. 1996
	C	Tracer	F, D	North America	Marine	Smith et al. 1996
	C, N	Diet	F, D	North America	Marine	Muir et al. 1995
Proboscidea	C, N	Diet	F, D	Africa	Terrestrial	Tieszen et al. 1989
	C	Diet	F, D	Asia	Terrestrial	Sukumar and Ramesh 1992
	C	Diet	F, D	Asia	Terrestrial	Sukumar et al. 1987
	C, N	Diet	F, D	Africa	Terrestrial	van der Merwe et al. 1990
	C	Diet	F, D	Africa	Terrestrial	van der Merwe et al. 1988
	C, N	Diet	F, D	Africa	Terrestrial	Vogel et al. 1990*a*
	C, N	Diet	F, D	Africa	Terrestrial	Vogel et al. 1990*b*
	C, N	Diet	F, D	Africa	Terrestrial	Koch et al. 1995
Hyracoidea	C	Diet	F, D	Africa	Terrestrial	DeNiro and Epstein 1978*b*
Sirenia	C	Diet	F, L, D	North America	Marine	Ames et al. 1996
Perissodactyla	C	Climate	F, D	North America	Terrestrial	MacFadden and Cerling 1994
Artiodactyla	C, N	Diet	F, D	Africa	Terrestrial	Ambrose and Deniro 1986
	C, N	Climate	F, D	North America	Terrestrial	Bada et al. 1990
	C, N	Climate	F, D	North America	Terrestrial	Cormie and Schwarcz 1996
	C, N	Climate	F, D	North America	Terrestrial	Cormie and Schwarcz 1994
	C	Paleontology	F, D	North America	Terrestrial	Hobson and Schwarcz 1986

Table A1 (*concluded*).

	C, N	Diet	F, D	Africa	Terrestrial	Thackeray et al. 1993
	C	Diet	F, D	Africa	Terrestrial	Vogel 1978
	C	Diet	F, D	Africa	Terrestrial	Tieszen et al. 1979
	C	Paleontology	F, D		Terrestrial	MacFadden 1997
	C	Tracer	F, D	North America	Terrestrial	Chisholm et al. 1986
Multiple[c]	C, N	Diet	F, D	Europe	Terrestrial	Bocherens et al. 1995
	C, N	Paleontology	F, D	Europe	Terrestrial	Bocherens et al. 1994
	C, N	Climate	F, D	Africa	Terrestrial	Heaton et al. 1986
	C	Diet	F, D	Africa	Terrestrial	Schoeninger and DeNiro 1982
	C	Paleontology	F, D	Africa	Terrestrial	Sillen 1988
Birds and mammals						
Multiple[c]	C, N	Method	E, L	North America	Terrestrial	DeNiro et al. 1985
	C, N	Food web	F, D	North America	Marine	Hobson and Welch 1992
	N	Pollution	F, D	North America	Marine	Jarman et al. 1997
	C, N	Pollution	F, D	North America	Marine	Jarman et al. 1996
	C, N	Food web	F, D	Antarctica	Marine	Rau et al. 1992
	C	Food web	F, D	North America	Marine	Schell and Ziemann 1989
	C, N	Diet	F, D		Marine and terrestrial	Schoeninger and Deniro 1984
	C, N	Diet	F, D	North America	Marine	Sydeman et al. 1997
	N	Food web	F, D	Africa	Terrestrial	Sealy et al. 1987

[a]C, carbon isotope ratios presented in the study; N, nitrogen isotope ratios presented in the study.
[b]B, field, laboratory, experimental, and descriptive; D, descriptive; E, experimental; F, field; L, laboratory.
[c]Study focused on more than one taxonomic order.

Table A2. Summary of data from the literature on stable carbon isotope values, stable nitrogen isotope values, diet, trophic chain, latitude, log body mass, and habitat moisture.

	Common name	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Tissue	Diet[a]	Trophic chain[b]	Latitude[c]	Mass[d]	Habitat moisture[e]	Study
Birds										
Struthioniformes										
Struthio camelus	Ostrich	–21.3		Bone	H_3	C_3	33	4.92		Von Schirnding et al. 1982
Podicipediformes										
Podiceps nigricollis	Eared Grebe	–26.3	9.1	Bone	I	C_3	36	2.47		Schoeninger and DeNiro 1984
Aechmophorus occidentalis	Western Grebe	–18.6	14.2	Bone	V	M	36	3.17		Schoeninger and DeNiro 1984
Sphenisciformes										
Aptenodytes patagonicus	King Penguin	–19.0	13.0	Bone	I	M	51	4.12		Schoeninger and DeNiro 1984
Pygoscelis papua	Gentoo Penguin	–16.1	10.7	Bone	V	M	51	3.77		Schoeninger and DeNiro 1984
Pygoscelis adeliae	Adelie Penguin		9.5	Bone	I	M	77	3.69		Mizutani et al. 1986
			5.9	Muscle	I	M	65	3.69		Rau et al. 1992
Eudyptes chrysolophus	Macaroni Penguin	–18.1	9.4	Bone	I	M	51	3.59		Schoeninger and DeNiro 1984
Spheniscus demersus	Jackass Penguin		16.1	Muscle	I		34			Sealy et al. 1987
Procellariiformes										
Diomedea nigripes	Black-footed Albatross	–18.2	14.4	Muscle	I	M	43	3.50		Gould et al. 1997[f]
Diomedea immutabilis	Laysan Albatross	–18.8	12.0	Muscle	I	M	43	3.48		Gould et al. 1997[f]
Macronectes giganteus	Southern Giant Fulmar		8.7	Muscle	V	M	65	3.66		Rau et al. 1992
Fulmarus glacialis	Northern Fulmar		17.4	Bone	V	M	74	2.74		Hobson 1993[f]
		–15.3	14.8	Bone	V	M	57	2.74		Thompson and Furness 1995[f]
			15.3	Muscle	V	M	74	2.74		Hobson 1993[f]
		–19.2	15.3	Muscle	V	M	74	2.74		Hobson and Welch 1992[f]

Table A2 (*continued*).

Fulmarus glacialoides	Antarctic Fulmar	–19.6	11.9	Bone	V	M	51	3.00	Schoeninger and DeNiro 1984
			6.7	Muscle	V	M	65	3.00	Rau et al. 1992
Thalassoica antarctica	Antarctic Petrel		5.6	Muscle	V	M	65	2.88	Rau et al. 1992
Daption capense	Cape Petrel		6.5	Muscle	V	M	65	2.63	Rau et al. 1992
Pagodroma nivea	Snow Petrel		7.2	Muscle	V	M	65	2.43	Rau et al. 1992
Pterodroma brevirostris	Kerguelan Petrel		7.8	Muscle	V	M	65	2.55	Rau et al. 1992
Halobaena caerulea	Blue Petrel		6.3	Muscle	V	M	65	2.31	Rau et al. 1992
Pachyptila vittata	Antarctic Prion		6.4	Muscle	V	M	65	2.29	Rau et al. 1992
Puffinus griseus	Sooty Shearwater		15.8	Bone	I	M	53	2.90	Hobson et al. 1994[f]
		–20.1	9.2	Muscle	I	M	38	2.90	Minami et al. 1995[f]
Puffinus tenuirostris	Short-tailed Shearwater	–23.0	8.0	Muscle	I	M	40	2.73	Minami et al. 1995[f]
Oceanites oceanicus	Wilson's Storm Petrel		8.3	Muscle	V	M	65	1.51	Rau et al. 1992[f]
Oceanodroma leucorhoa	Leach's Storm Petrel		17.1	Bone	V	M	56	1.60	Hobson et al. 1994[f]
		–21.2	13.8	Bone	V	M	56	1.60	Hobson et al. 1994[f]
Oceanodroma furcata	Fork-tailed Storm Petrel		17.9	Bone	V	M	53	1.74	Hobson et al. 1994[f]
			15.9	Muscle	V	M	53	1.74	Hobson et al. 1994[f]
Pelecaniformes									
Phaethon lepturus	White-tailed Tropicbird	–15.6		Muscle	V	M	18	2.52	Schaffner and Swart 1991
Fregata magnificens	Magnificent Frigatebird	–12.1	12.4	Bone	V	M	18	3.17	Schoeninger and DeNiro 1984
Sula capensis	Cape Gannett		13.7	Muscle	V	M	34	3.43	Sealy et al. 1987
Phalacrocorax capensis	Cape Cormorant		14.6	Muscle	V	M	34	3.08	Sealy et al. 1987
Phalacrocorax pelagicus	Pelagic Cormorant	–18.7	15.8	Muscle	V	M	55	3.27	Hobson et al. 1994[f]
Pelecanus occidentalis	Brown Pelican	–14.5	17.9	Bone	V	M	36	3.54	Schoeninger and DeNiro 1984
Ciconiiformes									
Ardea herodias	Great Blue Heron	–14.0	15.7	Muscle	V	M	40	3.38	Schoeninger and DeNiro 1984
Nycticorax nycticorax	Black-Crowned Night Heron	–20.9	10.1	Bone	V	C_3	36	2.95	Schoeninger and DeNiro 1984
Anseriformes									
Chen caerulescens	Snow Goose	–21.0	10.2	Muscle	H_3	C_3	29	3.42	Alisauskas and Hobson 1993[f]
Chen rossii	Ross' Goose	–24.7	7.5	Muscle	H_3	C_3	65	3.20	Hobson et al. 1993[f]
Chloephaga picta	Magellan Goose	–22.5	6.0	Bone	H_3	C_3	51	3.44	Schoeninger and DeNiro 1984
Somateria mollissima	Common Eider		15.7	Bone	I	M	75	3.32	Hobson 1993[f]
			13.2	Muscle	I	M	75	3.32	Hobson 1993[f]
		–20.3	8.1	Muscle	I	M	59	3.32	Broman et al. 1992[f]
Clangula hyemalis	Oldsquaw	–25.7		Muscle	I	M	70	2.94	Schell and Ziemann 1989
Melanitta perspicillata	Surf Scoter		11.8	Bone	I	M	54	2.98	Hobson et al. 1994[f]
Melanitta fusca	White-winged Scoter		12.2	Bone	I	M	54	3.24	Hobson et al. 1994[f]
Falconiformes									
Buteo lagopus	Rough-legged Hawk	–16.9	6.8	Bone	V	C_3	36	2.98	Schoeninger and DeNiro 1984
Gruiformes									
Rallus longirostris	Light-footed Clapper Rail	–18.4	17.9	Muscle	I	C_3	33	2.47	Kwak and Zedler 1997
Porzana carolina	Sora	–24.4	12.1	Muscle	H_3	C_3	33	1.87	Kwak and Zedler 1997
Charadriiformes									
Calidris melanotos	Pectoral Sandpiper	–27.9		Muscle	I	C_3	70	1.91	Schell and Ziemann 1989
Calidris pusilla	Semipalmated Sandpiper	–26.1		Muscle	I	C_3	70	1.50	Schell and Ziemann 1989

Table A2 (*continued*).

Phalaropus fulicaria	Red Phalarope	–27.3		Muscle	I	C_3	70	2.94		Schell and Ziemann 1989
Larus canus	Mew Gull		15.3	Muscle	V	M	55	2.61		Hobson et al. 1994[f]
Larus glaucescens	Glaucous-winged Gull	–15.0		Bone	I	M	49	3.00		Hobson 1987[f]
		–19.5	15.1	Muscle	I	M	55	3.00		Hobson 1993[f]
Larus occidentalis	Western Gull	–15.1		Bone	V	M	37	3.00		Hobson 1987[f]
Larus hyberboreus	Glaucous Gull		19.1	Bone	V	M	74	3.15		Hobson 1993[f]
		–17.6	17.0	Muscle	V	M	74	3.15		Hobson and Welch 1992[f]
Rissa tridactyla	Black-legged Kittiwake		17.2	Bone	V	M	74	2.61		Hobson 1993[f]
Sterna elegans	Elegant Tern	–18.8		Muscle	V	M	32	2.41		Schaffner and Swart 1991
Sterna paradisaea	Arctic Tern		5.9	Muscle	V	M	65	2.04		Rau et al. 1992
Sterna vittata	Antarctic Tern		5.4	Muscle	V	M	65	2.15		Rau et al. 1992
Alle alle	Dovekie		13.3	Bone	I	M	60	2.21		Hobson and Montevecchi 1991[f]
			12.9	Muscle	I	M	74	2.21		Hobson 1993[f]
Uria aalge	Common Murre		18.5	Bone	V	M	49	3.00		Hobson and Montevecchi 1991[f]
		–18.1	15.3	Muscle	V	M	55	3.00		Hobson et al. 1994[f]
Uria lomvia	Thick-billed Murre		17.3	Bone	V	M	74	2.98		Hobson 1993[f]
			15.8	Muscle	V	M	74	2.98		Hobson 1993[f]
		–18.4	15.8	Muscle	V	M	74	2.98		Hobson and Welch 1992[f]
Pinguinus impennis	Great Auk		15.8	Bone	V	M	49			Hobson and Montevecchi 1991[f]
Cepphus grylle	Black Guillemot		18.2	Bone	V	M	74	2.61		Hobson 1993[f]
			15.4	Muscle	V	M	74	2.61		Hobson 1993[f]
		–17.3	15.4	Muscle	V	M	74	2.61		Hobson and Welch 1992[f]
Cepphus columba	Pigeon Guillemot	–15.7	16.5	Muscle	V	M	48	2.69		Hobson et al. 1994[f]
Brachyramphus marmoratus	Marbled Murrelet	–16.5	15.3	Muscle	V	M	48	2.35		Hobson et al. 1994[f]
Brachyramphus brevirostris	Kittlitz's Murrelet		14.5	Muscle	I	M	59	2.35		Hobson et al. 1994[f]
Synthliboramphus antiquus	Ancient Murrelet	–16.4	15.0	Muscle	I	M	49	2.31		Hobson et al. 1994[f]
Ptychoramphus aleuticus	Cassin's Auklet		16.4	Bone	I	M	48	2.27		Hobson et al. 1994[f]
		–18.5	14.5	Muscle	I	M	48	2.27		Hobson et al. 1994[f]
Cyclorrhynchus psittacula	Parakeet Auklet		13.8	Muscle	I	M	55	2.42		Hobson et al. 1994[f]
Aethia cristatella	Crested Auklet		12.5	Muscle	I	M	55	2.42		Hobson et al. 1994[f]
Cerorhinca monocerata	Rhinoceros Auklet		17.6	Bone	V	M	48	2.72		Hobson et al. 1994[f]
		–17.3	15.9	Muscle	V	M	48	2.72		Hobson et al. 1994[f]
Fratercula corniculata	Horned Puffin	–20.3	13.3	Muscle	V	M	55	2.79		Hobson et al. 1994[f]
Fratercula cirrhata	Tufted Puffin	–18.5	14.7	Muscle	V	M	50	2.89		Hobson et al. 1994[f]
Strigiformes										
Tyto alba	Barn Owl	–21.2	9.7	Bone	V	C_3	36	2.73		Schoeninger and DeNiro 1984
Aegolius acadicus	Northern Saw-whet Owl	–18.9		Muscle	V	C_3	54	1.88		Hobson and Sealy 1991[f]
Passeriformes										
Calcarius lapponicus	Lapland Longspur	–27.0		Muscle	I	C_3	70	2.94		Schell and Ziemann 1989
Mammals										
Insectivora										
Erinaceus europaeus	Hedgehog	–20.8	9.4	Bone	I	C_3	49	2.84	Me	Bocherens et al. 1994[f]
Chiroptera										
Macrotus californicus	Leafnose bat	–19.6		Muscle	I	C_3	29	1.08	Me	Herrera et al. 1993
Eptesicus fuscus	Big brown bat	–19.5		Muscle	I	C_3	35	1.23	Me	Herrera et al. 1993
Antrozous pallidus	Pallid bat	–17.0		Muscle	I	C_3	35	1.32	Me	Herrera et al. 1993

Table A2 (*continued*).

Tadarida brasiliensis	Mexican freetail bat	–19.7		Muscle	I	C_3	26	1.06	Me	Herrera et al. 1993
Primates										
Cercopithecus mitis	Blue monkey	–19.4	5.9	Bone	H_3	C_3	2	3.83	Me	Ambrose and DeNiro 1986[f]
Colobus guerza	Black and white colobus	–18.8	5.6	Bone	H_3	C_3	2	4.01	Me	Ambrose and DeNiro 1986[f]
Papio anubius	Anubis baboon	–17.3	5.8	Bone	H_3	C_3	2	4.25		Ambrose and DeNiro 1986[f]
Papio cynocephalus	Chacma baboon	–19.3	6.1	Bone	O	C_3	30	4.28	Me	Thackeray et al. 1996
Rodentia										
Pedetes capensis	Springhare		8.0	Bone	H_3	C_3	34	3.49	Xe	Sealy et al. 1987
			8.8	Muscle	H_3	C_3	34	3.49	Xe	Sealy et al. 1987
Neotoma lepida	Wood rat	–14.4	5.8	Bone	H_3	C_3	36	2.16	Xe	Schoeninger and DeNiro 1984
Microtus townsendii	Field vole	–23.2		Bone	H_3	C_3	49	1.57	Me	Hobson and Schwarcz 1986
Hystrix africaeaustralis	Porcupine	–15.5	6.6	Bone	H_3	C_3	2	4.29	Me	Ambrose and DeNiro 1986[f]
Cetacea										
Tursiops truncatus	Bottle-nosed dolphin	–12.5	16.2	Bone	V	M	36	5.34		Schoeninger and DeNiro 1984
Delphinus delphis	Common dolphin	–13.9	15.5	Bone	V	M	36	4.76		Schoeninger and DeNiro 1984
		–17.8	14.8	Muscle	V	M	49	4.76		Ostrom et al. 1993
Lagenorhynchus albirostris	White-beaked dolphin	–18.1	16.2	Muscle	V	M	49	5.26		Ostrom et al. 1993
Lagenorhynchus obliquidens	Pacific white-sided dolphin	–12.2	15.1	Bone	V	M	36	4.79		Schoeninger and DeNiro 1984
Globicephala melas	Long-finned pilot whale	–18.0	13.3	Muscle	I	M	41	6.44		Abend and Smith 1997
Globicephala sieboldii	Short-finned pilot whale	–12.1	16.3	Bone	I	M	36	6.44		Schoeninger and DeNiro 1984
Lissodelphis borealis	Northern right whale dolphin	–18.7	11.8	Muscle	V	M		4.90		Gould et al. 1997[f]
Phocoena phoceona	Harbor porpoise	–11.6	16.6	Bone	V	M	36	4.78		Schoeninger and DeNiro 1984
Phocoenoides dalli	Dall's porpoise	–12.9	15.6	Bone	V	M	36	5.16		Schoeninger and DeNiro 1984
Delphinapterus leucas	Beluga whale	–14.1	16.8	Bone	V	M	60	5.91		Schoeninger and DeNiro 1984
		–18.1	16.6	Bone	V	M	74	5.91		Hobson and Welch 1992[f]
Modon monoceros	Narwhal	–18.0	15.8	Muscle	V	M	74	6.08		Hobson and Welch 1992[f]
Mesoplodon bidens	Sowerby's beaked whale	–18.5	11.7	Muscle	I	M	49	6.53		Ostrom et al. 1993
Kogia breviceps	Pygmy sperm whale	–17.2	11.9	Muscle	I	M	49	5.56		Ostrom et al. 1993
Eschrichtius robustus	Gray whale	–13.3	13.0	Bone	I	M	36	7.45		Schoeninger and DeNiro 1984
Balaenoptera acutorostrata	Minke whale	–14.0	14.4	Bone	I	M	36	6.95		Schoeninger and DeNiro 1984
		–18.3	12.3	Muscle	I	M	49	6.95		Ostrom et al. 1993
Balaenoptera physalus	Fin whale	–15.4	12.7	Bone	I	M	40	7.90		Schoeninger and DeNiro 1984
Balaenoptera musculus	Blue whale	–13.5	13.8	Bone	I	M	36	8.18		Schoeninger and DeNiro 1984
		–20.1	9.6	Muscle	I	M	49	8.18		Ostrom et al. 1993
Megaptera novaeangliae	Humpback whale	–18.7	13.4	Muscle	I	M	49	7.60		Ostrom et al. 1993
Balaena mysticetus	Bowhead whale	–15.9	14.5	Bone	I	M	65	8.04		Schoeninger and DeNiro 1984

Table A2 (*continued*).

Carnivora										
Alopex lagopus	Arctic fox	–20.6	5.9	Bone	V	C_3	60	3.54	Me	Schoeninger and DeNiro 1984
		–17.7		Bone	V	C_3	66	3.54	Me	Angerbjorn et al. 1994[f]
Canis aureus	Golden jackal	–8.7	11.4	Bone	V	C_4	2	0.97	Xe	Ambrose and DeNiro 1986[f]
Canis lupus	Wolf	–20.6	9.9	Bone	V	C_3	65	4.53	Me	Bocherens et al. 1994[f]
Otocyon megalotis	Bat-eared fox	–8.6	17.2	Bone	I	C_4	2	3.62	Xe	Ambrose and DeNiro 1986[f]
Ursus americanus	Black bear	–20.8	4.9	Bone	O	C_3	45	5.13	Me	Bocherens et al. 1994[f]
Ursus arctos	Brown bear	–20.2	6.9	Bone	O	C_3	41	5.25	Me	Bocherens et al. 1994[f]
Ursus maritimus	Polar bear	–15.7		Bone	V	M	61	5.48		Ramsay and Hobson 1991[f]
		–18.0	21.1	Muscle	V	M	75	5.48		Hobson and Welch 1992[f]
Procyon lotor	Racoon	–22.8	11.0	Bone	I	C_3	45	3.77	Me	Bocherens et al. 1994[f]
Mustela vison	Mink	–16.0	16.5	Muscle	V	C_3	57	2.94	Me	Ben-David et al. 1997*b*
Martes foina	Stone marten	–20.7		Bone	V	C_3	51	3.00	Me	Grupe and Kruger 1990[f]
Martes martes	Pine marten	–20.3		Bone	V	C_3	51	3.14	Me	Grupe and Kruger 1990[f]
Martes pennanti	Fisher	–20.9	6.7	Bone	V	C_3	55	3.43	Me	Bocherens et al. 1994[f]
Mellivora capensis	Honey badger	–14.7	10.8	Bone	V	C_4	2	3.89	Xe	Ambrose and DeNiro 1986[f]
Enhydra lutris	Sea otter	–9.8	14.2	Bone	I	M	40	2.43		Schoeninger and Deniro 1984
Genetta genneta	Genette	–20.0	10.8	Bone	V	C_3	65	3.21		Bocherens et al. 1994[f]
Ichneumia albicauda	White-tailed mongoose	–10.1	12.7	Bone	I	C_4	2	3.63	Xe	Ambrose and DeNiro 1986[f]
Crocuta crocuta	Spotted hyena	–6.9	11.2	Bone	V	C_4	2	4.84	Xe	Ambrose and DeNiro 1986[f]
Felis concolor	Mountain lion	–17.6	7.6	Bone	V	C_3	36	4.69		Schoeninger and DeNiro 1984
Lynx canadensis	Bobcat	–15.8	10.0	Bone	V	C_3	36	3.97		Schoeninger and DeNiro 1984
Lynx rufus	Lynx	–22.4	6.2	Bone	V	C_3	55	3.98	Me	Bocherens et al. 1994[f]
Panthera tigris	Tiger	–18.0	8.1	Bone	V	C_3	20	5.05	Me	Schoeninger and DeNiro 1984
Panthera pardus	Leopard	–7.1	10.2	Bone	V	C_4	2	4.63		Ambrose and DeNiro 1986[f]
Panthera leo	Lion	–5.7	9.8	Bone	V	C_4	2	5.24	Xe	Ambrose and DeNiro 1986[f]
Acinonyx jubatus	Cheetah	–12.7	10.1	Bone	V	C_4	2	4.69	Xe	Ambrose and DeNiro 1986[f]
Pinnipedia										
Callorhinus ursinus	Northern fur seal	–18.9	16.6	Muscle	V	M	57	5.04		Hobson et al. 1997*c*
Arctocephalus gazella	Antarctic fur seal		7.8	Muscle	I	M	65	4.97		Rau et al. 1992
Arctocephalus pusillus	Cape fur seal		17.6	Bone	V	M	34	5.03		Sealy et al. 1987
			19.4	Muscle	V	M	34	5.03		Sealy et al. 1987
Eumetopias jubatus	Northern sea lion	–18.2	17.5	Muscle	V	M	60	5.83		Hobson et al. 1997*c*[f]
Zalophus californianus	California sea lion	–12.7	19.3	Bone	V	M	40	4.88		Schoeninger and DeNiro 1984
Odobenus rosmarus	Walrus	–13.9	12.3	Bone	I	M	60	6.03		Schoeninger and DeNiro 1984
		–18.7	11.7	Muscle	I	M	65	6.03		Muir et al. 1995[f]
Lobodon carcinophagus	Crabeater seal		5.9	Muscle	I	M	65	5.36		Rau et al. 1992
Hydrurga leptonyx	Leopard seal		7.7	Muscle	V	M	65	5.74		Rau et al. 1992
Ommatophoca rossii	Ross' seal		9.1	Muscle	I	M	65	5.48		Rau et al. 1992
Erignathus barbatus	Bearded seal	–16.6	16.8	Muscle	I	M	74	5.39		Hobson and Welch 1992[f]

Table A2 (*continued*).

Phoca groenlandica	Harp seal	–15.2	15.6	Bone	V	M	50	5.19		Schoeninger and DeNiro 1984
Phoca hispida	Ringed seal	–16.2		Bone	V	M	63	5.01		Ramsay and Hobson 1991[f]
		–17.3	17.3	Muscle	V	M	74	5.01		Hobson and Welch 1992[f]
Phoca vitulina	Harbor seal	–12.3	17.6	Bone	V	M	36	5.04		Schoeninger and DeNiro 1984
		–17.6	18.6	Muscle	V	M	60	5.04		Hobson et al. 1997*c*[f]
Proboscidea										
Elephas maximus	Asian elephant	–18.6		Bone	H_3	C_3	18	6.40	Me	Sukumar and Ramesh 1992
Loxodonta africana	African elephant	–18.4	13.8	Bone	H_3	C_3	0	6.40	Me	Tieszen et al. 1989
Hyracoidea										
Procavia capensis	Hyrax	–11.0		Bone	H_3	C_3	3	3.51	Xe	DeNiro and Epstein 1978*b*
Heterohyrax brucei	Gray hyrax	–20.0		Bone	H_3	C_3	3	3.48	Xe	DeNiro and Epstein 1978*b*
		–17.0	9.2	Bone	H_3	C_3	2	3.48	Xe	Ambrose and DeNiro 1986[f]
Perissodactyla										
Equus zebra	Mountain zebra	–11.8		Bone	H_4	C_4		5.46	Me	Vogel 1978
Equus burchelli	Burchell's zebra	–8.3	6.7	Bone	H_4	C_4	2	5.33	Me	Ambrose and DeNiro 1986[f]
Ceratotherium simum	White rhinoceros	–10.2		Bone	H_4	C_4		5.26	Me	Vogel 1978
Artiodactyla										
Potamochoerus porcus	Bushpig	–18.0	7.1	Bone	O	C_3	2	4.74	Me	Ambrose and DeNiro 1986[f]
Hylochoerus meinertzhageni	Giant forest hog	–24.4	4.3	Bone	H_3	C_3	2	5.15	Me	Ambrose and DeNiro 1986[f]
Phacochoerus aethiopicus	Warthog	–8.8	7.4	Bone	H_3	C_3	2	4.83	Me	Ambrose and DeNiro 1986[f]
		–10.6		Muscle	H_3	C_3	22	4.83	Me	Vogel 1978
Hippopotamus amphibius	Hippopotamus	–8.4	8.3	Bone	H_4	C_4	2	6.15	Me	Ambrose and DeNiro 1986[f]
Odocoileus hemionius	Mule deer	–22.0	5.8	Bone	H_3	C_3	26	4.66	Me	Schoeninger and DeNiro 1984
		–20.6		Bone	H_3	C_3	41	4.66	Me	Hobson and Schwarcz 1986
Odocoileus virginianus	White-tailed deer	–21.3	4.8	Bone	H_3	C_3	55	4.76	Me	Cormie and Schwarcz 1994
Rangifer tarandus	Reindeer	–19.6	1.9	Bone	H_3	C_3	65	5.03	Me	Bocherens et al. 1994[f]
		–28.7		Muscle	H_3	C_3	70	5.03	Me	Schell and Ziemann 1989
Giraffa camelopardalis	Giraffe	–20.0	6.9	Bone	H_3	C_3	2	6.00	Xe	Ambrose and DeNiro 1986[f]
Tragelaphus angasi	Nyala	–18.7		Bone	H_3	C_3		4.88		Vogel 1978
Tragelaphus scriptus	Bushbuck	–21.2	6.6	Bone	H_3	C_3	2	4.70	Me	Ambrose and DeNiro 1986[f]
Tragelaphus strepsiceros	Greater kudu	–21.1		Bone	H_3	C_3	18	5.29	Xe	Sillen 1988[f]
Tragelaphus imberbis	Lesser kudu	–21.1		Bone	H_3	C_3	25	5.13	Xe	Vogel 1978
Tragelaphus euryceros	Bongo	–25.0	5.2	Bone	H_3	C_3	2	5.52	Me	Ambrose and DeNiro 1986[f]
Taurotragus oryx	Eland	–18.3	8.0	Bone	H_3	C_3	2	5.56	Xe	Ambrose and DeNiro 1986[f]
Syncerus caffer	Buffalo	–11.0	6.3	Bone	H_4	C_4	2	5.70	Me	Ambrose and DeNiro 1986[f]
Bison bison	Bison	–20.5	4.4	Bone	H_3	C_3	60	5.83	Xe	Bocherens et al. 1994[f]
		–19.3		Bone	H_3	C_3	52	5.83	Xe	Chisholm et al. 1986
Sylvicapra grimmia	Duiker	–21.2		Bone	H_3	C_3	14	4.21	Me	van der Merwe et al. 1988
		–19.8	5.9	Bone	H_3	C_3	2	4.21	Me	Ambrose and DeNiro 1986[f]

Table A2 (*concluded*).

Kobus ellipsiprymnus	Waterbuck	–9.5	7.3	Bone	H_4	C_4	2	5.20	Me	Ambrose and DeNiro 1986[f]
Redunca arundinum	Reedbuck	–6.4		Bone	H_4	C_4	18	4.65	Me	Sillen 1988[f]
Redunca redunca	Bohor reedbuck	–8.9	7.1	Bone	H_4	C_4	2	4.60	Me	Ambrose and DeNiro 1986[f]
Redunca fulvorofula	Mountain reedbuck	–8.0	6.4	Bone	H_4	C_4	2	4.49	Me	Ambrose and DeNiro 1986[f]
Hippotragus equinus	Roan antelope	–13.6		Bone	H_4	C_4		5.40		Vogel 1978
Oryx gazella	Gemsbok	–11.5		Bone	H_3	C_3	22	5.32	Xe	Vogel 1978
		–12.1		Muscle	H_3	C_3	22	5.32	Xe	Vogel 1978
Damaliscus dorcas	Bontebok	–8.0		Bone	H_4	C_4		4.79	Xe	Vogel 1978
Damaliscus lunatus	Topi	–6.8		Bone	H_4	C_4	25	5.11		van der Merwe et al. 1988
Alcephalus buselaphalus	Hartebeest	–9.2		Bone	H_4	C_4	34	5.13	Me	Vogel 1978
		–10.5		Muscle	H_4	C_4	34	5.13	Me	Vogel 1978
Sigmoceros lichtensteinii	Lichtenstein's hartebeest	–6.5		Bone	H_3	C_3	14	5.24	Me	van der Merwe et al. 1988
Connochaetes gnou	Black wildebeest	–7.3		Bone	H_4	C_4	27	5.26	Xe	van der Merwe et al. 1988
Connochaetes taurinus	Blue wildebeest	–6.9	7.9	Bone	H_4	C_4	27	5.27	Xe	Ambrose and DeNiro 1986[f]
		–9.0		Bone	H_4	C_4		5.27	Xe	Vogel 1978
Oreotragus oreotragus	Klipspringer	–18.8	10.0	Bone	H_3	C_3	2	4.08	Xe	Ambrose and DeNiro 1986[f]
Ourebia ourebi	Oribi	–8.2		Bone	H_3	C_3		4.10		Vogel 1978
Raphicerus campestris	Steenbok		6.1	Bone	H_3	C_3		4.05	Xe	Sealy et al. 1987
		–17.6	7.1	Bone	H_3	C_3	2	4.05	Xe	Ambrose and DeNiro 1986[f]
			5.7	Muscle	H_3	C_3		4.05	Xe	Sealy et al. 1987
Raphicerus melanotis	Cape grysbok	–23.1		Bone	H_4	C_4		4.02	Xe	Vogel 1978
Madoqua kirki	Kirk's dik dik	–18.9	9.4	Bone	H_3	C_3	2	4.74	Xe	Ambrose and DeNiro 1986[f]
Aepyceros melampus	Impala	–9.4	8.0	Bone	H_4	C_4	2	4.70	Me	Ambrose and DeNiro 1986[f]
		–15.5		Muscle	H_4	C_4	25	4.70	Me	Vogel 1978
Gazella thomsoni	Thompson's gazelle	–12.0	9.7	Bone	H_4	C_4	2	4.34	Xe	Ambrose and DeNiro 1986[f]
Gazella granti	Grant's gazelle	–18.2	8.9	Bone	H_3	C_3	2	4.70	Xe	Ambrose and DeNiro 1986[f]
Antidorcas marsupialis	Springbok		15.9	Bone	H_3	C_3		4.59	Xe	Sealy et al. 1987
		–18.1		Bone	H_3	C_3	34	4.59	Xe	Vogel 1978
			15.6	Muscle	H_3	C_3		4.59	Xe	Sealy et al. 1987
Rupicapra rupicapra	Chamois	–20.4	2.6	Bone	H_3	C_3	43	4.18	Me	Bocherens et al. 1994[f]
Ovibus moschatus	Muskox	–20.6	5.9	Bone	H_3	C_3	65	2.32	Me	Bocherens et al. 1994[f]

[a]H_3, herbivores that eat C_3 plants; H_4, herbivores that eat C_4 plants; V, carnivores that eat vertebrates; I, carnivores that eat invertebrates; O, omnivores that eat both plants and animals.

[b]Trophic chain on which the species relies: C_3, C_4, or marine (M).

[c]When two values are give for latitude, the first was used to relate $\delta^{13}C$ values of bone and the second to relate $\delta^{13}C$ values of muscle. Units are degrees of latitude.

[d]Log body mass.

[e]Estimated for terrestrial mammals only: Xe, species uses xeric habitats; Me, species uses mesic habitats.

[f]Lipids were extracted from sample, otherwise no treatment of lipids was indicated in the Methods.