Use of stable isotopes to determine diets of living and extinct bears

G.V. Hilderbrand, S.D. Farley, C.T. Robbins, T.A. Hanley, K. Titus, and C. Servheen

Abstract: The potential use of stable-isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) to estimate bear diets was assessed in 40-day feeding trials using American black bears (*Ursus americanus*). Bear plasma and red blood cells have half-lives of ~4 days and ~28 days, respectively. The isotopic signature of bear plasma is linearly related to that of the diet, and with the exception of adipose tissue, there is no isotopic fractionation across bear tissues. Isotopic analyses were used to estimate the diets of three bear populations: Pleistocene cave bears (*U. speleaus*) in Europe, grizzly bears (*Ursus arctos horribilis*) inhabiting the Columbia River drainage prior to 1931, and brown bears (*U. arctos*) of Chichagof and Admiralty islands, Alaska. Cave bears were omnivores with terrestrially produced meat contributing from 41 to 78% (58 ± 14%) of their metabolized carbon and nitrogen. Salmon contributed from 33 to 90% (58 ± 23%) of the metabolized carbon and nitrogen in grizzly bears from the Columbia River drainage. Finally, most brown bears on Chichagof and Admiralty islands feed upon salmon during the late summer and fall; however, a subpopulation of bears exists that does not utilize salmon.

Résumé : Le potentiel des analyses au moyen d'isotopes stables ($\delta^{13}C$ et $\delta^{15}N$) pour estimer le régime alimentaire des ours a été evalué au cours d'expériences d'alimentation d'une durée de 40 jours chez des Ours noirs (*Ursus americanus*). Le plasma des ours a une demi-vie de ~4 jours et leurs érythrocytes, une demi-vie de ~28 jours. La signature isotopique du plasma est en relation linéaire avec celle du régime alimentaire; de plus, à l'exception de ce qui prévaut dans le tissu adipeux, il n'y a pas de fractionnement isotopique dans les tissus de l'ours. Des analyses au moyen d'isotopes ont été utilisées pour étudier le régime alimentaire chez trois populations d'ours : des ours des cavernes du Pléistocène (*U. speleaus*) en Europe, des Grizzlis (*Ursus arctos horribilis*) du bassin du Columbia d'avant 1931 et des Ours bruns (*U. arctos*) des îles Chichagof et Admiralty, en Alaska. Les ours des cavernes étaient des omnivores et consommaient de la chair d'animaux terrestres leur fournissant de 41 à 78% (58 ± 14%) de leur carbone et azote métabolisables. Les saumons fournissaient aux Grizzlis du bassin du Columbia de 33–90% de leur carbone et azote métabolisables. Enfin, la plupart des Ours bruns des îles Chichagof et Admiralty se nourrissent de saumon à la fin de l'été et à l'automne; cependant, une sous-population de ces ours survit sans consommer de saumons.
[Traduit par la Rédaction]

Introduction

Food habits of bears have been studied by scat analyses and direct observation of foraging behavior. Scat analyses, even when corrected for differential disappearance, almost always estimate diet at the level of the population rather than at that of the individual or subpopulation (e.g., males versus females), cannot be used for foods that are completely digested and produce no quantifiable residues (e.g., meat), and do not indicate the nutritional importance of different foods. Fecal correction factors used to convert scat analyses to actual food habits can be very difficult to estimate. For example, bears frequently avoid consuming the skin of large mammals, and other carnivores may use the same carcass. A correction factor for large-mammal residues in a bear consuming ungulates varies 18-fold when the consumption of skin and hair ranges from 5 to 100% (Hewitt 1989).

Stable-isotope analyses, e.g., carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), of bear tissues can complement fecal analyses by overcoming the above weaknesses, as well as indicate the historical diet of dead bears and the current and past diets of living bears. Carbon isotope analyses of animal tissue indicate the relative contributions of marine and terrestrial sources to the animal's carbon pool (DeNiro and Epstein 1978; Ramsey and Hobson 1991; Hobson and Welch 1992). In marine ecosystems, carbon enters as bicarbonate and ^{13}C is enriched relative to terrestrial ecosystems where carbon enters as CO_2 (Peterson and Fry 1987). Nitrogen isotope analyses indicate the trophic position of the consumer. ^{15}N is enriched relative to ^{14}N at each step in a food chain (DeNiro and Epstein 1980; Minagawa and Wada 1984; Hobson and Welch 1992), probably because of the preferen-

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tial excretion of the lighter ^{14}N in urinary waste products (Peterson and Fry 1987).

Thus, the objectives of the experimental portion of this study were to determine (*i*) the relationship between carbon and nitrogen isotope ratios in bear tissues relative to ratios found in the diet, and (*ii*) the turnover time of isotopes in different bear tissues relative to dietary change. Finally, to illustrate the ecological applications of isotopic analyses, we determined the trophic level of extinct European cave bears (*Ursus spelaeus*), the importance of salmon to early grizzlies (*Ursus arctos horribilis*) of the Pacific Northwest, and the spring and summer diets of brown bears (*U. arctos*) on Chichagof and Admiralty islands, southeast Alaska.

Cave bear trophic level

Cave bears were 2½ to 3 times larger than modern brown bears, presumably hibernated as do other temperate-zone bears, and, based on dental and jaw structure, are hypothesized to have been the most herbivorous of all bears (Kurten 1976). However, the herbivore hypothesis seems untenable, owing to the poor digestibility of vegetation by bears (Dierenfeld et al. 1982; Pritchard and Robbins 1990). Rates of gain by bears are lower on vegetation than on more digestible dietary items such as meat or berries (C.T. Robbins, unpublished data). Additionally, the small size of most wild fruits produces relatively small bite sizes and harvest rates, so the maximum bear size attainable on most wild fruits is only a fraction of the size of an adult cave bear (Welch et al).[1] Thus, we hypothesize that cave bears were omnivores like most other temperate-zone bears, but because of their large size were specialized for feeding on megafauna, including carrion.

Historical use of salmon by Pacific Northwest grizzly bears

Columbia River salmon populations have been reduced by hydroelectric dams and irrigation projects impeding or completely blocking their migration routes; by mining, road construction, and logging suffocating spawning streams with silt, debris, or toxic chemicals; and by overfishing (Lantz 1967; Fulton 1968, 1970; Platts 1970). Current research and management efforts are directed towards recovery of both salmon populations and their spawning areas (Volkmann and McConnaha 1993).

The grizzly bear, which is listed as threatened under the Endangered Species Act of 1975, was one of the organisms that historically fed on spawning salmon (Davis et al. 1986). Two of the six proposed grizzly bear recovery areas are the North Cascades of Washington and the Bitterroot Ecosystem of Idaho (Servheen 1984). The North Cascades' runs of chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon (*O. nerka*), coho salmon (*O. kisutch*), and steelhead trout (*Salmo gairdneri*) and the Bitterroot Ecosystem's runs of chinook salmon and steelhead trout have been depleted by human activities and development (Fulton 1968, 1970). Information on the historical importance of salmon in the diet of grizzly bears would benefit the drafting and implementation of grizzly bear recovery plans.

[1] C.A. Welch, J. Keay, K.C. Kendall, and C.T. Robbins. Constraints to frugivory by bears. Submitted for publication.

Seasonal diets of brown bears on Chichagof and Admiralty islands

Telemetry data collected from brown bears on Chichagof and Admiralty islands suggest that a subpopulation exists which geographically has access to spawning salmon but does not utilize salmon as a food resource (K. Titus, unpublished data). However, because of the difficulty or expense of continuously monitoring bear locations, one can never be certain that a specific bear did not visit a stream containing salmon. Stable-isotope analyses of bear tissue can determine if a specific bear utilized salmon as a food resource.

Methods

Sample collection

Feeding trials were conducted at the Washington State University Bear Research, Conservation, and Education Center in 1994. Experimental groups consisting of three American black bears (*Ursus americanus*) were fed one of seven experimental diets (Table 1) for 40 days during which blood samples were collected every 10 days. The mixed diets were formulated to provide 35 and 65% of their digestible dry matter from either herring or beef, with vegetable matter providing the rest. Dry matter digestibilities of the mixed-diet ingredients were determined according to Pritchard and Robbins (1990). The plant matter in the mixed diets was derived from C_3 plants, which are depleted in ^{13}C relative to C_4 plants. Temperate-zone and subarctic bears such as cave bears, American black bears, and brown or grizzly bears fed or feed almost exclusively on C_3 plants, whereas C_4 plants could contribute significantly to the diets of tropical bears such as the sloth bear and sun bear (Raven et al. 1986).

To assess isotopic fractionation between consumer tissues, plasma, red blood cells, hair, claws, adipose tissue, muscle, skin, and bone collagen were collected from three domestic rabbits (*Oryctolagus cuniculus*), three laboratory mice (*Mus musculus*), and three yearling American black bears. The rabbits and mice were raised on a single diet (R and R Rabbit Pellets 781 and Rat and Mouse Standard Expanded, Beekay Feeds) from birth to the time of sampling, while the bears were fed a single diet (Dealer's Pride, Purina) for the 7 months prior to sampling.

Bone samples from 10 cave bears were obtained from the American Museum of Natural History, New York, the National Museum of Natural History, Washington, D.C., and the Bulgarian Museum of Natural History, Sofia. Original collection sites included France, Czechoslovakia, Bulgaria, and Italy. Bone samples from four extinct, similarly aged herbivores (woolly rhinoceros (*Coelodonta antiquitatus*), woolly mammoth (*Mammuthus primigenius*), auroch (*Bos primigenius*), and horse/zebra (*Equus* sp.)) from Denmark, Hungary, and Italy were also obtained from collections at the same museums.

All federal, state, and university museums in the United States that house ursid collections were surveyed (Choate and Genoways 1975). Of the approximately 2500 grizzly specimens listed, 11 had been collected between 1890 and 1931 from the Columbia River drainage of Washington, Oregon, and Idaho (American Museum of Natural History, New York; National Museum of Natural History, Washington D.C.; University of Montana, Missoula). One of the 11 bears is a type specimen and therefore was not available for sampling. Samples of bone (n = 9; cranial material) and hair (n = 3) were collected from the 10 remaining specimens. Bone (n = 5) and hair (n = 1) samples were also obtained from grizzly bears that were collected in central Montana and eastern Wyoming between 1856 and 1888. The latter bears did not have access to salmon during their lifetime. Finally, bone samples (n = 5) were obtained from southeastern Alaska coastal brown bears (1916–1921) that had access to abundant salmon.

Fig. 1. Representative isotope equilibration curves for plasma (*a* and *b*) and red blood cells (*c* and *d*) of American black bears when a dietary change occurs. Dietary changes were as follows: bear chow to 35% herring : 65% vegetation (*a* and *b*), salmon to apples (*c*), and 35% herring : 65% vegetation to mule deer (*d*).

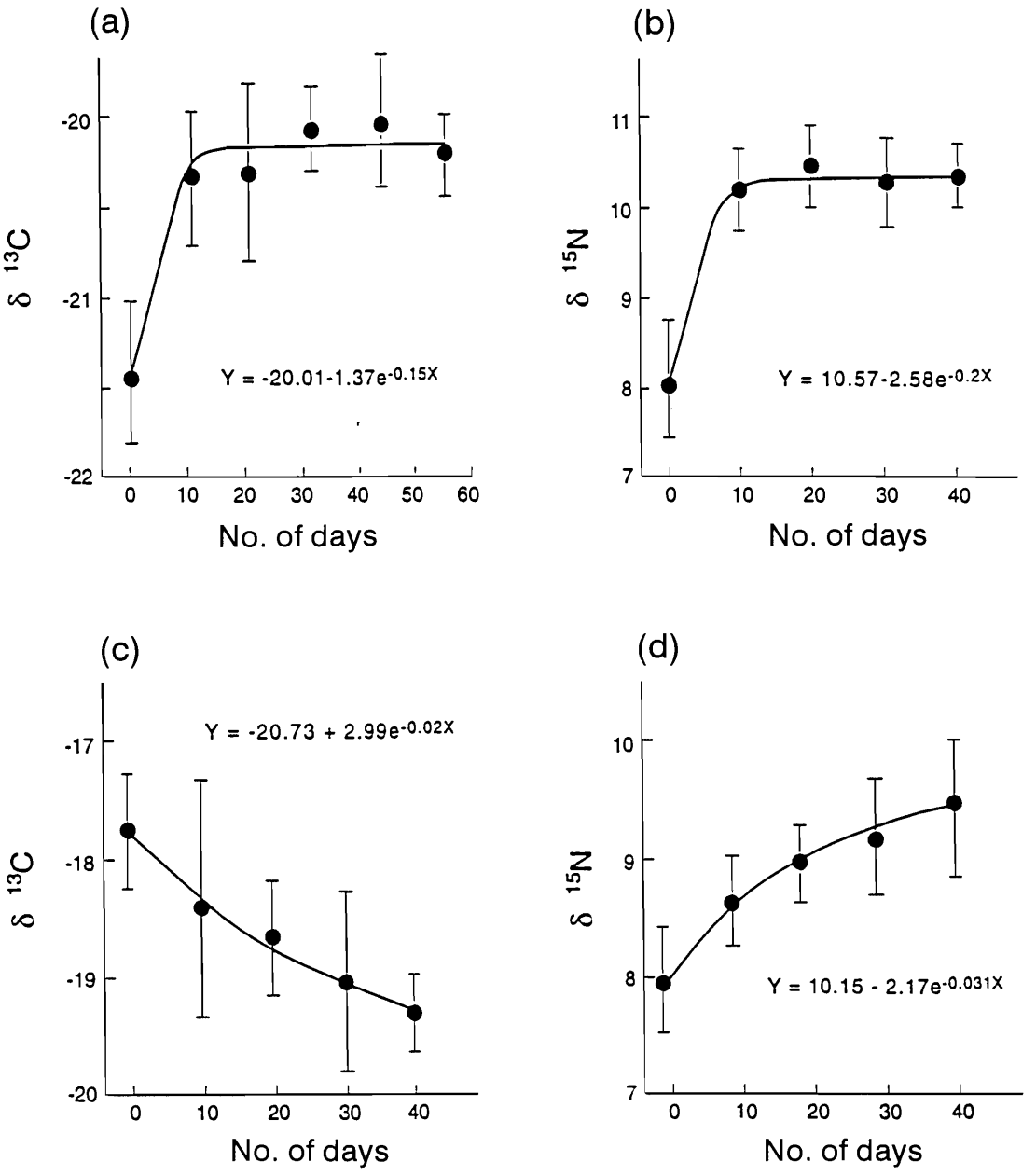


Table 1. Diets fed to American black bears during 40-day feeding trials.

Diet	$\delta^{13}C$	$\delta^{15}N$
Salmon (*Oncorhynchus tshawytscha*)	−20.1	11.2
Mule deer (*Odocoileus hemionus*)	−26.2	6.4
Apples (*Malus* sp.)	−24.1	2.3
46.6% alfalfa, 42.7% herring meal, 5.6% wheat, 5.0% honey, 0.1% vitamix	−21.8	9.5
72.4% alfalfa, 17.9% herring meal, 5.6% wheat, 5.0% honey, 0.1% vitamix	−22.4	5.8
53.3% alfalfa, 39.7% beef meal, 5.0% honey, 1.9% fat, 0.1% vitamix	−22.3	4.4
77.1% alfalfa, 15.9% beef meal, 5.0% honey, 1.9% fat, 0.1% vitamix	−22.1	2.9

Eleven blood and 7 hair samples were collected between June 24 and July 1, 1994, from 11 brown bears inhabiting Chichagof and Admiralty islands. Spawning salmon are abundant in the streams of these islands during the late summer and fall, but the returning salmon had not yet arrived when these samples were collected. An additional five hair samples were obtained from bears captured on

Fig. 2. Relationship between ^{13}C signatures of the diet and of equilibrated plasma in American black bears (●) and polar bears (▲; Hobson and Welch 1992). SEE, standard error of the estimate.

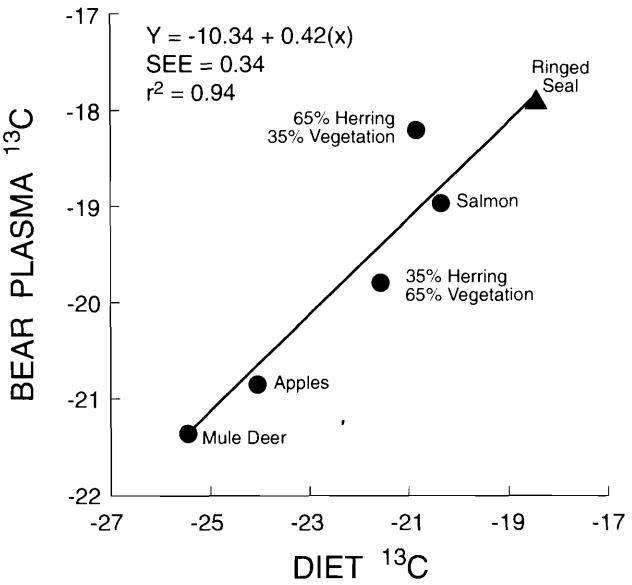
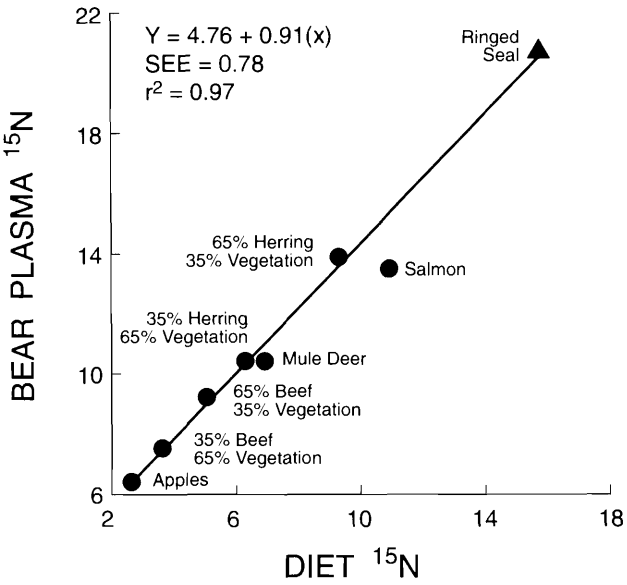


Fig. 3. Relationship between ^{15}N signatures of the diet and that of equilibrated plasma in American black bears (●) and polar bears (▲; Hobson and Welch 1992). SEE, standard error of the estimate.



Admiralty Island between 1981 and 1992. The latter bears were suspected to be alpine bears that did not use salmon.

Sample analyses

Lipids were extracted from hair, skin, and muscle with a chloroform–ether solvent. Collagen was extracted from bone according to Chisholm et al. (1983). All samples were then freeze-dried and ground to <1 mm. For ^{13}C analysis, 25 mg of sample and 0.5 g of CuO were placed in a 6-mm Vycor tube, flame-sealed under vacuum, and baked at 550°C for 6 h (Hobson and Clark 1992*a*). Carbon dioxide from the combusted sample was then collected and purified using successive dry ice – methanol and liquid nitrogen traps. To assess ^{15}N content, 10 mg of sample was mixed with 4 g of CuO, 3 g of Cu, and 0.4 g of CaO, placed in a 9-mm Vycor tube, flame-sealed under vacuum, and baked at 850°C for 2 h (Fiedler and Proksch 1975). Collected samples were then analyzed for carbon and nitrogen isotope content using a Finnigan MAT δS mass spectrometer. Results are reported as ratios relative to PeeDee limestone (^{13}C) or atmospheric nitrogen (^{15}N) as follows:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N and the R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio (Peterson and Fry 1987). Mixed-diet isotopic signatures (Table 1) are weighted averages based on the product of the digestible dry matter and isotopic ratios of each ingredient.

Results

Captive bear feeding trials

Carbon and nitrogen isotope ratios in bear plasma equilibrated with the diet within 10 days, whereas the isotope ratios of red blood cells continued to change after 40 days (Fig. 1). The half-life of the plasma was less than 4 days, whereas the half-life of the red blood cells averaged 28 days. Carbon and nitrogen isotope ratios in bear plasma were linearly related to the carbon and nitrogen isotope ratios of single-item diets and the weighted, available dietary carbon and nitrogen ratios in mixed diets (Figs. 2, 3). As hypothesized, plasma from bears consuming terrestrially produced plants or animals was much less enriched with ^{13}C than that of bears consuming food from marine sources (Fig. 2). Similarly, ^{15}N concentrations of bear plasma increased with increasing trophic level (Fig. 3). Finally, all tissues except fat (ANOVA, $p < 0.0001$) have the same isotopic enrichment when animals are on a constant diet (Fig. 4). Thus, the isotopic relationships between diet and plasma (Figs. 2, 3) also apply to hair, bone collagen, and red blood cells.

The dietary sources of assimilated carbon and nitrogen can be estimated by first determining the magnitude of the marine component. The marine salmon component (percent digestible dry matter) of a bear's diet can be estimated as

$$[1] \quad M = \frac{^{13}C + 24.1}{4.0} \times 100$$

where ^{13}C is the estimated isotope ratio of the diet when the equation in Fig. 2 is solved for X, $-24.1 \pm 1.3‰$ (reported as the mean ± standard deviation) is the average temperate-zone plant and animal terrestrial signature (Chisholm and Schwartz 1982; Tieszen et al. 1983; this study), and $4.0 \pm 0.5‰$ is the difference between the average terrestrial signature and the average signature ($-20.1 \pm 1.0‰$) for four species of salmon (chinook salmon, coho salmon, chum salmon (*O. keta*), and pink salmon (*O. gorbuscha*)) (M. Ben-David, unpublished data; this study).

Once the marine salmon component has been determined, the dietary contribution of carbon and nitrogen absorbed from terrestrially produced meat (T_m, %) can be estimated by

$$[2] \quad T_m = \left[\frac{^{15}N - (M \times 11.5) - 2.3}{4.1} \times (1 - M)\right] \times 100$$

where ^{15}N is the estimated nitrogen enrichment of the diet when the equation in Fig. 3 is solved for the measured iso-

Fig. 4. Isotopic signatures of tissues collected from laboratory mice, domestic rabbits, and American black bears fed a constant diet for either 7 months (bears) or throughout life (rabbits and mice).

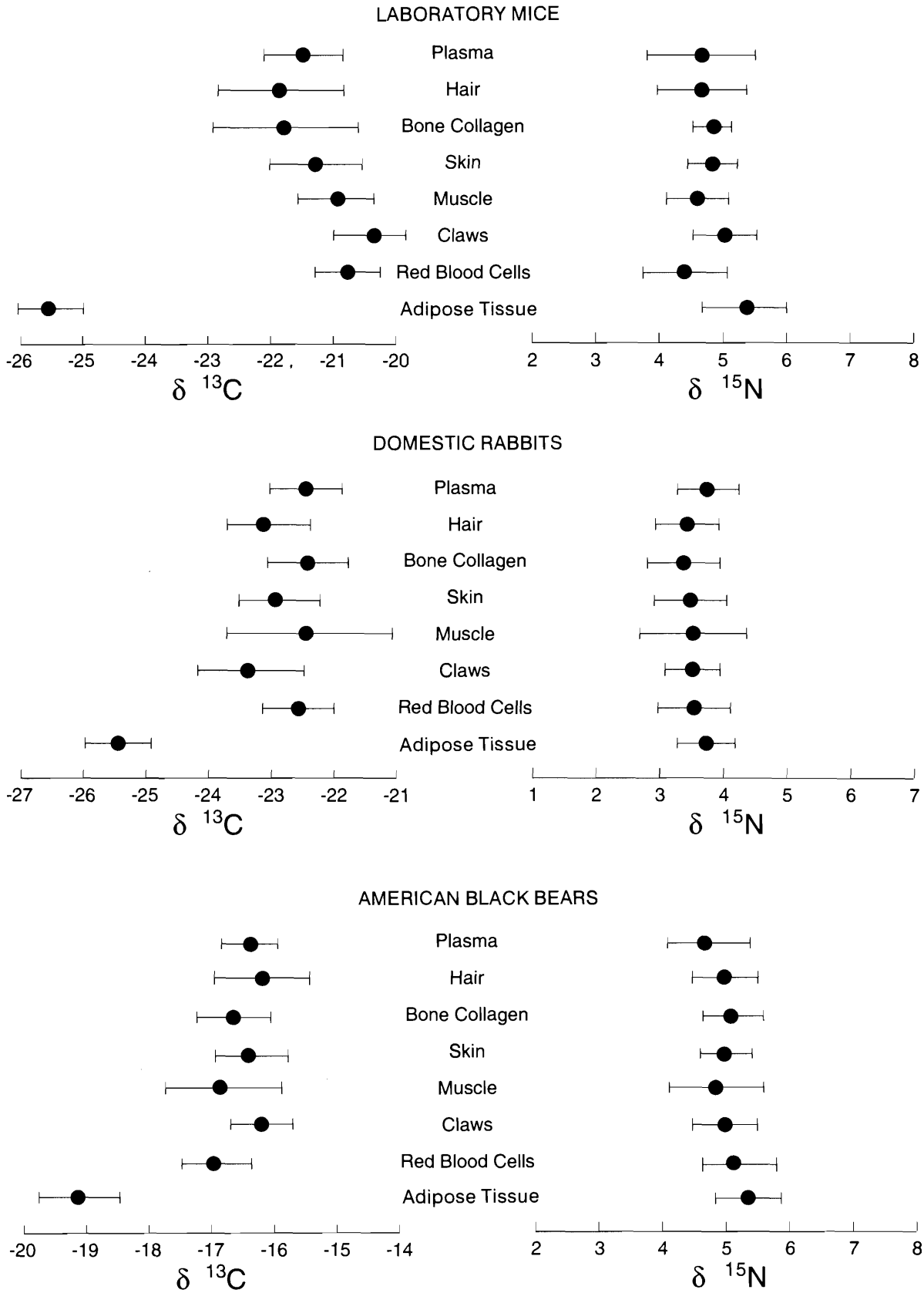


Fig. 5. Isotopic signatures of bone collagen extracted from cave bears (▲) and Pleistocene herbivores (●).

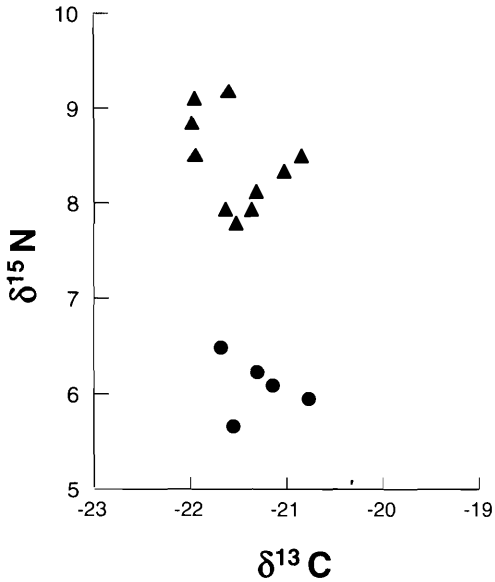
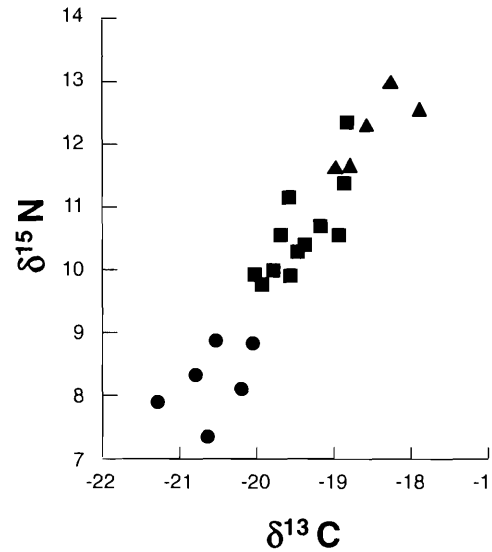


Fig. 6. Carbon and nitrogen enrichment of hair and bone collected from grizzly bears killed between 1856 and 1931 in eastern Wyoming and central Montana (●), the Columbia River drainage (■), and coastal southeast Alaska (▲).



tope ratio of the bear's diet, M is the marine dietary contribution in decimal form, 11.5 ± 0.4‰ is the average ^{15}N signature of four species of salmon (Mathisen et al. 1988; Kline et al. 1990; M. Ben-David, unpublished data; this study), 2.3 ± 0.6‰ is the average ^{15}N signature of terrestrial plant matter (DeNiro and Epstein 1980; this study), and 4.1 ± 0.5‰ is the average difference in ^{15}N enrichment between primary producers (plants) and their consumers (Minagawa and Wada 1984; Sholto-Douglas et al. 1991; Hobson and Welch 1992; this study). Finally, the proportion of carbon and nitrogen absorbed from terrestrial plant matter is 100 minus the sum of the marine and terrestrially produced meat contributions.

Cave bear trophic level

Cave bear bones are significantly enriched (t test, $p < 0.0001$) with ^{15}N ($\bar{x}$ = 8.4 ± 0.5‰) relative to the four herbivore bones ($\bar{x}$ = 6.2 ± 0.3‰), but there is no difference in ^{13}C (Fig. 5). When eq. 2 is used to predict the amount of meat in the cave bear's diet with the mean terrestrial plant signature reduced from 2.3‰ to 1.6‰, the average based on solving the equation in Fig. 3 for the observed nitrogen enrichments in the four herbivores, meat provided 58 ± 14% (range 41–78%) of all metabolized carbon and nitrogen absorbed by cave bears.

Historical use of salmon by Pacific Northwest grizzly bears

Grizzly bears collected from coastal Alaska and the Columbia River drainage were significantly enriched in ^{13}C and ^{15}N relative to those collected from eastern Wyoming and central Montana (t test, $p < 0.0002$) (Fig. 6). Salmon contributed 33–90% (58 ± 23%) of the carbon and nitrogen assimilated from the historical diet of grizzly bears living in the Columbia River drainage (Fig. 7). Terrestrially produced meat (e.g., ungulates, rodents, and insects) contributed 0–21% (8 ± 11%) and plant matter contributed 10–64% (34 ± 19%) of metabolized carbon and nitrogen. Grizzly bears from central Montana and eastern Wyoming obtained their assimilated carbon and nitrogen from terrestrially produced meat (13–54%, 35 ± 15%) and plant matter (46–87%, 65 ± 15%), while coastal Alaskan bears obtained virtually all of their carbon and nitrogen from salmon (94 ± 9%).

Seasonal diets of brown bears on Chichagof and Admiralty islands

The carbon and nitrogen isotope signatures of red blood cells collected during the early summer prior to the annual return of spawning salmon are much less enriched than the hair that grows from late June through September, when the salmon are present (Fig. 8). The absorbed carbon and nitrogen used to produce the red blood cells was derived from terrestrial plants (85 ± 15%), terrestrially produced meat (14 ± 16%), and salmon (1 ± 2%). The values contrast with the sources of the carbon and nitrogen in the hair (34 ± 27% from terrestrial plants, 11 ± 21% from terrestrially produced meat, 55 ± 34% from salmon) for those bears with significant ^{13}C enrichment. However, as hypothesized, a subpopulation of bears does exist that maintained a year-long terrestrial diet.

Discussion

Captive bear feeding trials

Owing to different turnover rates, the isotopic signatures of different consumer tissues serve as windows to different dietary periods. Plasma provides an indication of an animal's diet during the week prior to sampling, while red blood cells reflect the diet of the consumer over the past 2–3 months (Hobson and Clark 1992*b*; this study). Hair signatures are representative of the diet during the period of hair growth, which begins in midsummer and continues throughout the fall, while collagen, because of its long turnover rate, can be used to indicate a yearly or lifetime diet (e.g., van

Fig. 7. Locations and estimated contributions of salmon, terrestrially produced meat, and plant matter (values are given in this order) to the assimilated carbon and nitrogen pool of grizzly bears killed in the northwestern United States between 1856 and 1931. Values in parentheses are from hair samples; all other values are from bone collagen. Idaho's Bitterroot Ecosystem and Washington's North Cascades grizzly bear recovery areas are indicated.

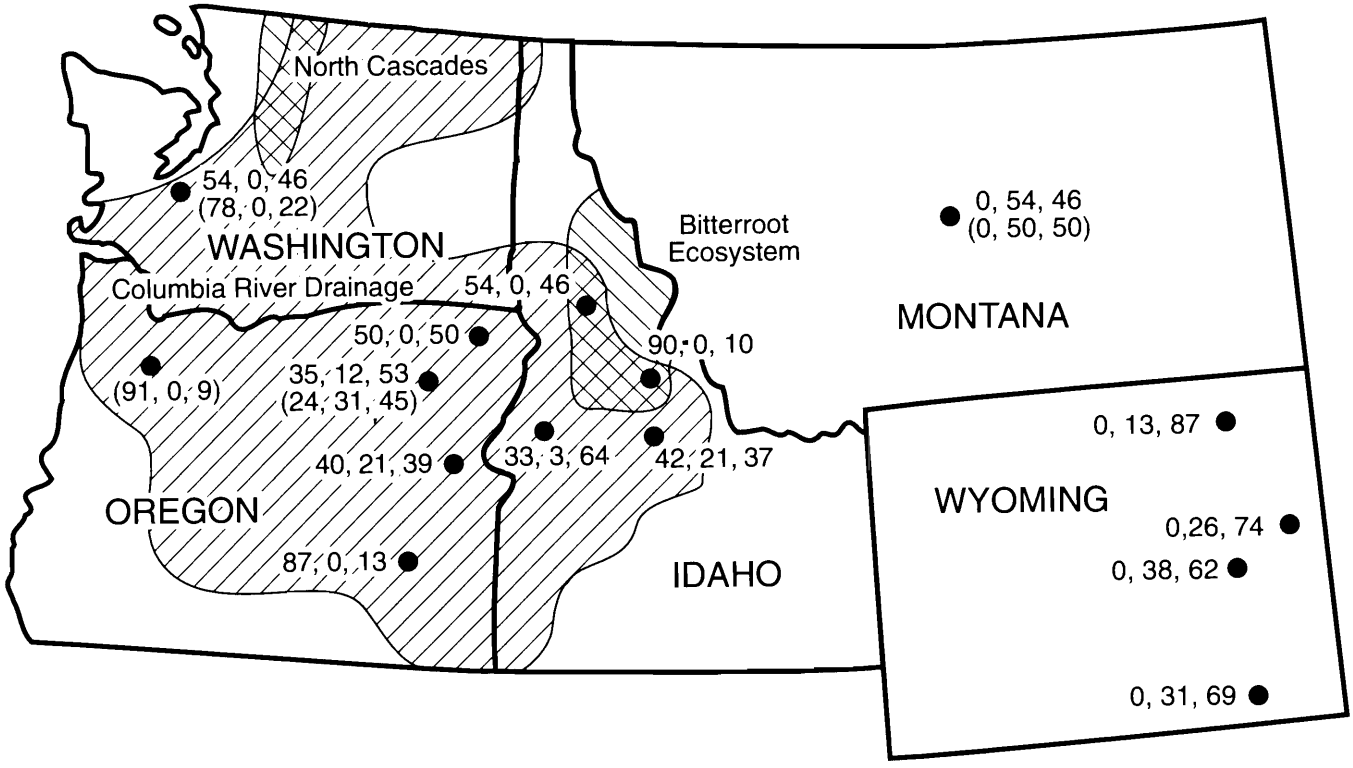
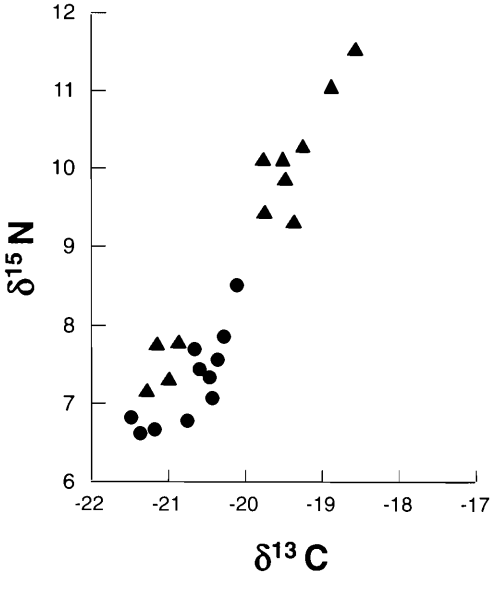


Fig. 8. Carbon and nitrogen enrichment of hair (▲) and red blood cells (●) collected from brown bears on Chichagof and Admiralty islands, Alaska.



der Merwe and Vogel 1978; Stenhouse and Baxter 1979; Chisholm and Schwarcz 1982; Tieszen et al. 1989; Hobson and Montevecchi 1991; Loken et al. 1992).

Equilibrated bear plasma was enriched in ^{13}C from 0.4 to 4.5 at dietary values of −18.5 to −25.5‰. Hobson and Clark (1992*a*) reported enrichment values in various quail tissues ranging from 0.2‰ (liver) to 2.7‰ (collagen). An enrichment in ^{15}N of 4.1 ± 0.8‰ over the diet was present in equilibrated bear plasma. Similar ^{15}N enrichments at each increase in trophic level have been reported by DeNiro and Epstein (1980), Minagawa and Wada (1984), and Hobson and Welch (1992). The depletion of ^{13}C in adipose tissue relative to other tissues analyzed has been reported elsewhere (DeNiro and Epstein 1977; Tieszen et al. 1983; Hobson 1995).

Cave bear trophic level

Bocherens et al. (1994) concluded that cave bears were primarily herbivores, because of low ^{15}N enrichments. While collagen ^{15}N levels in Pleistocene herbivores reported by Bocherens et al. (1994) (6.6 ± 0.7‰) did not differ from those reported in this study (6.2 ± 0.3‰), their reported levels for cave bears spanned two entire trophic levels, with signatures ranging from that characteristic of a plant (3.4‰) to that of a true carnivore (9.3‰). Similarly, Bocherens et al.'s (1994) ^{15}N levels for living (1.9−5.9‰) and extinct (3.8−7.4‰) herbivores were not sufficiently different from the lower limit of living (6.2−9.9‰) and extinct (8.0‰) carnivores to have identified an omnivore. Known omnivores in their data set, such as brown and black bears, had nitrogen enrichments (3.8−8.7‰) that are very similar to the enrichments they reported for cave bears. Thus, owing to the variation in their ^{15}N results, Bocherens et al.'s (1994) conclusion that cave bears were herbivores is untena-

ble. Matheus (1995) and Bocherens et al. (1995) have constructed trophic models of bear populations based on isotopic signatures. When applied to the current data, both models show a clear distinction between herbivores and the cave bears in this study, and support the hypothesis that cave bears were omnivores.

Kurten (1976) concluded that the cause of cave bear extinction, which occurred 11 000 years ago (Brown 1993), is unknown. However, the extinction of the cave bear mirrored the extinction of large herbivores (Kurten 1968). The loss of this major source of dietary carbon and nitrogen would have been extremely detrimental to such a large omnivore and was likely the most important factor contributing to its extinction.

Historical use of salmon by Pacific Northwest grizzly bears

While the recovery of historic spawning areas would benefit grizzly bear populations reintroduced to regions with reduced salmon runs, salmon are not essential for bear survival (Davis et al. 1986). In other ecosystems lacking salmon as a food resource, grizzly bears feed on vegetation, insects, ungulates, freshwater fish, and small mammals (Hamer et al. 1991; Mattson et al. 1991; Clevenger et al. 1992). However, studies have identified a strong positive correlation between the autumn mass of female bears and their reproductive success during hibernation (Rogers 1976; Stringham 1990). Bears' reproduction rate, one of the slowest of any terrestrial mammal (Bunnell and Tait 1981), is a critical factor in long-term population viability. Because spawning salmon are more nutrient dense than virtually any other food resource available to bears in the Pacific Northwest, grizzly bear recovery would be enhanced by simultaneous salmon recovery in the North Cascades and Bitterroot Ecosystem.

Seasonal diets of brown bears on Chichagof and Admiralty islands

Brown bears of Chichagof and Admiralty islands feed exclusively on food from terrestrial sources during spring and early summer. Upon the arrival of spawning salmon in the late summer and fall, most of the brown bears shift their diet to include salmon. However, four bears analyzed did not utilize the returning salmon and may be representative of a subpopulation that survives on a wholly terrestrial diet.

In summary, stable-isotope analyses offer insight into the biology of both living and dead bears. The ability to determine the proportions of meat and (or) vegetation in a bear's diet during various time intervals from samples collected during a single capture can lead to a more comprehensive understanding of the nutritional ecology of individual bears and bear populations than is possible using more conventional scat analyses or direct observation alone.

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