Major components of grizzly bear diet across North America

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Abstract: We measured stable carbon and nitrogen isotope ratios in guard hair of 81 populations of grizzly bears (*Ursus arctos* L., 1758) across North America and used mixing models to assign diet fractions of salmon, meat derived from terrestrial sources, kokanee (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)), and plants. In addition, we examined the relationship between skull size and diet of bears killed by people in British Columbia. The majority of carbon and nitrogen assimilated by most coastal grizzly bear populations was derived from salmon, while interior populations usually derived a much smaller fraction of their nutrients from salmon, even in areas with relatively large salmon runs. Terrestrial prey was a large part of the diet where ungulates were abundant, with the highest fractions observed in the central Arctic, where caribou (*Rangifer tarandus* (L., 1758)) were very abundant. Bears in some boreal areas, where moose (*Alces alces* (L., 1758)) were abundant, also ate a lot of meat. Bears in dryer areas with low snowfall tended to have relatively high meat diet fractions, presumably because ungulates are more abundant in such environments. Kokanee were an important food in central British Columbia. In areas where meat was more than about a third of the diet, males and females had similar meat diet fractions, but where meat was a smaller portion of the diet, males usually had higher meat diet fractions than females. Females reached 95% of their average adult skull length by 5 years of age, while males took 8 years. Skull width of male grizzly bears increased throughout life, while this trend was slight in females. Skull size increased with the amount of salmon in the diet, but the influence of terrestrial meat on size was inconclusive. We suggest that the amount of salmon in the diet is functionally related to fitness in grizzly bears.

Résumé : Nous avons mesuré les rapports des isotopes stables de carbone et d'azote dans des poils de garde provenant de 81 populations de grizzlis (*Ursus arctos* L., 1758) largement réparties en Amérique du Nord et nous avons utilisé des modèles de mélange pour attribuer les fractions du régime alimentaire correspondant au saumon, à la viande d'origine terrestre, au kokani (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) et aux plantes. De plus, nous avons examiné la relation entre la taille du crâne et le régime alimentaire chez des ours tués par les humains en Colombie-Britannique. La plus grande partie du carbone et de l'azote assimilés par la plupart des populations côtières de grizzlis provient du saumon, alors que, chez les populations de l'intérieur des terres, une fraction beaucoup plus faible des nutriments provient du saumon, même dans les régions où les montaisons de saumons sont importantes. Les proies terrestres forment une partie considérable du régime là où les ongulés sont abondants et les proportions les plus importantes s'observent dans la région arctique centrale où les caribous (*Rangifer tarandus* (L., 1758)) sont très nombreux. Les ours de certaines régions boréales riches en orignaux (*Alces alces* (L., 1758)) consomment aussi beaucoup de viande. Les ours qui habitent les régions plus sèches aux précipitations de neige réduites tendent à avoir des fractions importantes de viande dans leur régime, probablement parce que les ongulés sont généralement plus nombreux dans ces environnements. Les kokanis sont un élément significatif du régime dans le centre de la Colombie-Britannique. Dans les régions où la viande constitue plus d'environ le tiers du régime, les mâles et les femelles ont des régimes de composition semblable; cependant, là où la viande représente une plus petite fraction du régime, les mâles ont généralement une fraction de viande plus élevée dans leur régime que les femelles. Les femelles atteignent 95 % de leur longueur moyenne de crâne vers l'âge de cinq ans, alors que les mâles n'y arrivent qu'à huit ans. La largeur du crâne des grizzlis mâles augmente tout au cours de la vie, alors que cette tendance est peu marquée chez les femelles. La taille du crâne augmente en fonction de la quantité de saumon dans le régime, mais l'effet de la viande d'origine terrestre sur la taille n'est pas clair. Nous croyons que la quantité de saumon dans le régime chez les grizzlis est fonctionnellement reliée à la fitness.

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Introduction

The amount of meat in a grizzly bear's (*Ursus arctos* L., 1758) diet is related to a bear's fitness in the short term through its influence on the bear's nutritional state and over the long term through its influence on the bear's body size (Hilderbrand et al. 1999*a*, 1999*b*). Choosing a meat-based diet may increase fitness in situations where larger bears have greater fitness than smaller conspecifics. But when protein availability is unpredictable, being larger may have a fitness cost. When protein availability is low, smaller bears are better able to meet their maintenance requirements by feeding on plants (Welch et al. 1997; Rode et al. 2001). Even when protein availability is predictable enough for many bears to have a largely protein-based diet, females with young may be able to increase their inclusive fitness by feeding primarily on plants when they can acquire enough nutrients for hibernation without having to expose their young to potentially predatory males on salmon spawning streams (Ben-David et al. 2004). It also appears that protein has a seasonal influence on size whereby bears that eat high-protein diets in spring and summer primarily add muscle mass, while high-protein diets eaten in fall are largely stored as lipids (Hilderbrand et al. 1999*b*). Berries are largely carbohydrates and when eaten in the fall, they allow bears to add the fat required for denning, although larger bears are less able to maintain mass on a pure berry diet (Welch et al. 1997). The addition of higher protein foods to a berry diet increases muscle mass gain (Rode and Robbins 2000; Felicetti et al. 2003*a*).

Protein in the diet is also important to grizzly bears at the population level because it is related to litter size and population density (Hilderbrand et al. 1999*a*). We wanted to expand on Hilderbrand et al.'s work (1999*a*) on the diet–density relationship by (*i*) considering the current continuous range of grizzly bears, (*ii*) considering the application of the relationship to the prediction of carrying capacity, (*iii*) evaluating how different protein sources influence the size of individual bears, and (*iv*) increasing our understanding of the functional relationship between fitness and carrying capacity.

Diet estimates based on scat analyses (*i*) underestimate meat in the diet (Robbins et al. 2004), (*ii*) cannot always be assigned to species, (*iii*) can only rarely be assigned to an individual, thus precluding comparisons between diet and individual fitness measures, (*iv*) do not measure assimilated nutrients, and (*v*) would be difficult to carry out at the continental scale because of the effort required to collect representative scat samples. Analysis of stable isotopes in bear hair samples is less influenced by these problems. Stable isotopes measure the assimilated nutrients for the elements examined. Representative hair samples are easily obtained from both passive hair snags, such as those routinely used during DNA-based inventories, and the inspection of hunter-killed bears. Hair can be assigned to the correct species and individual by analyzing DNA extracted from the root of the hair (Paetkau 2003). Guard hairs are grown between late spring and fall, thus integrating the diet over much of the ac-

tive season of temperate-dwelling bears (Hilderbrand et al. 1996; Felicetti et al. 2003*b*). The components of an animal's diet are estimated by comparing the isotope ratios of diet items to that of the consumer using a mixing model (Phillips and Gregg 2001). These models assume that mass is conserved as it moves through trophic levels and that the isotope ratio of the consumer's tissue is a linear combination of diet isotope ratios.

We collected grizzly bear hair samples from the field and from other researchers and analyzed them for stable carbon and nitrogen isotope ratios (i.e., $\delta^{13}C$ and $\delta^{15}N$). We combined those data with previously published data to describe bear diet. Our first objective was to describe the pattern of marine and terrestrially derived meat in the diet of grizzly bears across North America. Second, we compared bear size with the amount of marine and terrestrial meat in the diet to test the hypothesis that size increases with the amount of meat in the diet. We predicted that bears would achieve adult size at similar ages and we compared size and bear age to test this prediction and to facilitate the examination of diet and size.

Methods

Isotope analysis

We analyzed the stable nitrogen and carbon isotope composition of grizzly bear hair from 81 areas across the current continuous range of the species in North America. We assumed that our diet estimate was an average of the bears' annual diet because we used only whole guard hairs. We used data from the published and unpublished literature (Table S1[2]) and from 1242 samples that we obtained and prepared ourselves. Three groups of samples from the literature consisted of hair and bone (Jacoby et al. 1999), but since isotopic signatures for two of these groups were similar to concurrently published hair data for the same area (Hilderbrand et al. 1999*a*), we used combined hair and bone data to increase sample sizes. Most samples were collected by other researchers from clearly laid out study areas. However, some samples came from mandatory submissions of human-killed bears from Alaska, British Columbia, Northwest Territories, and Nunavut. We grouped samples by areas with similar life histories to generate a mean signature for each local population. No $\delta^{13}C$ measurements were available for four study areas but because no salmon were found in those areas, diet could be determined from $\delta^{15}N$ values alone (see below). We excluded cubs but did not exclude bears killed by wildlife control officers because (on average) these bears did not have higher isotopic signatures than other bears from the same area, in contrast to the findings of Hobson et al. (2000).

Hair was cleaned by soaking it for 2 h in a 2:1 chloroform–methanol solution; it was then rinsed in distilled water and air dried. One or more hairs totaling 1 mg (0.8–1.2 mg) were put into a tin cup and analyzed commercially at University of California, Davis. Measurement error, variation among repeated measures of hairs from within the same sample, and variation among hairs taken from different areas

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of the body were not large enough to mask variation among bears or among years.

Two control samples were analyzed after every 12 hair samples, and measurement error was 0.05 (SD) for $\delta^{13}C$ and 0.12 for $\delta^{15}N$ ($n = 103$), which was lower than the variation among repeated samples. Variation in signatures among hairs from the same hair sample — hairs that presumably came from similar locations on the same bear — was $SD_{13C} = 0.22$ and $SD_{15N} = 0.52$ ($n = 66$). Variation in signatures among samples collected on different dates within a year, and presumably from somewhat different locations on the same bear, was higher ($SD_{13C} = 0.60$, $SD_{15N} = 0.70$, $n = 51$). We analyzed paired samples from the back and the rump of eight live-captured bears from the Yukon north slope, and variation among signatures was small ($SD_{13C} = 0.11$, $SD_{15N} = 0.33$, $n = 16$). Variation among years was similar to other measurement errors ($SD_{13C} = 0.67$, $SD_{15N} = 1.21$, $n = 14$) except in the Owikeno Sound, where there was a major decline in salmon abundance (Boulanger et al. 2004; $SD_{13C} = 1.44$, $SD_{15N} = 2.64$, $n = 33$).

We derived a population mean by weighting the mean for each sex. Males often consume more meat than females (Jacoby et al. 1999; Hobson et al. 2000; Ben-David et al. 2004) but rarely make up more than 40% of the population (McLellan et al. 1999; McLoughlin et al. 2003; Schwartz et al. 2003). We weighted the female isotopic signature to make up 60% of the population's diet estimate for those populations for which we had sex data for all samples. In four areas where we did not have complete sex data, we used an unweighted mean. In 10 cases the population mean was based on data for only one sex (usually female).

Estimation of diet

We estimated the contributions of four diet components — plants, marine-derived nutrients (primarily salmon), terrestrial meat (primarily ungulates), and landlocked kokanee salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) — to grizzly bear diets by comparing stable carbon and nitrogen isotope ratios of bear hair and potential diet types. Stable isotope ratios in consumers are higher than those in their diet because organisms preferentially assimilate the heavier isotope or respire the lighter isotope (Hilderbrand et al. 1996). We accounted for the preferential assimilation (fractionation) of ^{15}N by correcting (i.e., increasing) the measured isotope ratios of potential diet groups according to the equation determined by Felicetti et al. (2003b). The equation documents a decrease in ^{15}N fractionation with a decrease in the $^{15}N/^{14}N$ ratio of the diet. We did not use their equation for $\delta^{13}C$ because the fit was weaker and the equation implied that at $\delta^{13}C$ values greater than $-18.7‰$, the consumer's tissue would be depleted in ^{13}C (i.e., have a lower $\delta^{13}C$ value than their diet). This seemed unlikely, based on other investigations of fractionation of carbon in hair (Hobson et al. 1996; Roth and Hobson 2000; Ayliffe et al. 2004). Instead, we increased $\delta^{13}C$ values of terrestrial and freshwater diet components by 2‰ and that of the marine component (salmon) by 1‰, after Ben-David et al. (2004). We reduced all hair $\delta^{13}C$ values by 1.5‰ because hair is enriched in ^{13}C compared with blood and muscle and the above fractionation values were for blood or muscle. Ben-David et al. (2004) suggested correcting hair by 1–2‰ compared with blood, which is

supported by work on foxes, seals, and horses (Hobson et al. 1996; Roth and Hobson 2000; Ayliffe et al. 2004).

We calculated fractions for diet components using 7 different methods. Methods 1–4 were used for systems where there were only two main components in the diet. We used a simple, single-isotope linear mixing model similar to eq. 3 in Hobson et al. (2000) but based on $\delta^{15}N$ values instead of $\delta^{13}C$ values. The main places where this approach was used were coastal areas, where salmon and plants were the two main diet components (method 1, $n = 19$), and much of the eastern (method 2, $n = 17$), northern (method 3, $n = 8$), and central (method 4, $n = 13$) range of grizzly bears, where ungulates and plants were the main diet components.

Methods 5 and 6 were used where a population was thought to have a diet composed of three components. Here, we used the program Isoerror (Phillips and Gregg 2001) to calculate diet fractions from the observed $\delta^{13}C$ and $\delta^{15}N$ values if the mean for the population fell in the Euclidean space of the diet components (method 6, $n = 12$). If the mean isotope measures for the population fell outside the Euclidean space, we used method 5 ($n = 6$), after Hilderbrand et al. (1996):

$$[1] \qquad M = (\delta^{13}C_{bear} - \delta^{13}C_{terr})/(\delta^{13}C_{salmon} - \delta^{13}C_{terr})$$

where M is the fraction of a bear's diet consisting of salmon or other marine-derived food, $\delta^{13}C_{bear}$ is the $\delta^{13}C$ value measured in bear hair, $\delta^{13}C_{terr}$ is the average $\delta^{13}C$ value in all terrestrial plant and animal foods, increased for fractionation (we used the generalized plant endpoint), and $\delta^{13}C_{salmon}$ is the average $\delta^{13}C$ value for salmon, also corrected for fractionation. We assumed salmon was the main marine-derived food of grizzly bears; other potential foods such as eulachon (*Thaleichthys pacificus* (Richardson, 1836)) and other fishes, seals, whales, and invertebrates have similar isotopic signatures (Kelly 2000; Kurle and Worthy 2001; Ben-David et al. 2004).

All isotopic diet endpoints except the plant endpoint were derived from appropriate data in the literature. Terrestrial meat signatures were derived for broad areas in which we assumed bears would use similar ungulate prey (Table 1). We determined $\delta^{13}C_{plant}$ by inserting -23 (SD = 0.35, $n = 91$) for $\delta^{13}C_{bear}$ into eq. 1 above. This value was the mean $\delta^{13}C_{bear}$ for four populations in the west slopes of the Rocky Mountains (Parsnip Mountains, Columbia Mountains, and central and southern Selkirk Mountains) that are known to eat little terrestrial meat (Hobson et al. 2000; Ciarniello et al. 2003) and have no salmon available. The mean $\delta^{13}C$ values for bears that had $\delta^{15}N$ values < 3.7‰ were similar among various regions of the continent (Table 2). We used the mean $\delta^{15}N$ value from the above areas, plus 1 SD to allow for variation among areas and individuals, to identify bears that ate little meat.

For method 5 we calculated the amount of terrestrial meat in the diet using eq. 2 in Hilderbrand et al. (1996):

$$[2] \qquad T = \left(\frac{\delta^{15}N_{bear} - M\delta^{15}N_{salmon} - \delta^{15}N_{plant}}{\delta^{15}N_{terr} - \delta^{15}N_{plant}} \right)(1 - M)$$

where T is the fraction of a bear's diet consisting of terrestrial meat, $\delta^{15}N_{bear}$ is the isotope ratio measured in bear hair (reduced for trophic fractionation), $\delta^{15}N_{plant}$ is the average

Table 1. Observed isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) and isotopic endpoints ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$) used to calculate relative measures of major diet components of grizzly bears (*Ursus arctos*) across western North America.

Food type	$\delta^{13}C$ (‰)	$\Delta\delta^{13}C$	SD	$\delta^{15}N$ (‰)	$\Delta\delta^{15}N$	SD	n	Sources
Terrestrial meat								
Arctic and subartic tundra	–22.3	–20.3	1	3.1	8.0	1	57	Barnett 1994; Gau 1998; Ben-David et al. 2001; B. Milakovic, personal communication
Boreal	–23.5	–21.5	1	2.1	7.1	1	35	Szepanski et al. 1999; Ben-David et al. 2001; Kielland 2001; B. Milakovic, personal communication
North coast	–24.8	–22.8	1	2.5	7.5	1	107	Jacoby et al. 1999; Szepanski et al. 1999; Ben-David et al. 2004
Temperate mountains	–25.3	–23.3	1	3.4	8.3	1	70	Jacoby et al. 1999; Hobson et al. 2000; Felicetti et al. 2005; B. Milakovic, personal communication
Fish								
Kokanee	–31.0	–29.0	1.5	6.7	11.2	1.2	3	Tom Johnston, BC Ministry of Water, Lands and Air Protection, Vancouver, British Columbia
Anadromous salmon	–19.9	–18.9	1	12.5	16.3	1	338	Bilby et al. 1996; Hildebrand et al. 1996; Jacoby et al. 1999; Satterfield and Finney 2002; Ben-David et al. 2004
Plants								
Generalized plant baseline	–26.6	–24.6	2	–2.8	2.8	3	200	Derived using data from areas where there is little meat in the diet; see text

Note: $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ values have been adjusted for trophic-level fractionation.

Table 2. Mean isotope values for bears with $\delta^{15}N < 3.7$‰, which is the mean value for bears in four study areas where bears were known to eat little meat, plus one standard deviation (see text), in five ecozones of western North America (Commission for Environmental Cooperation 1997).

Ecozone	$\delta^{13}C$ (‰)	SD	$\delta^{15}N$ (‰)	SD	n
Temperate mountains	–23.0	0.37	2.8	0.63	142
Sub-boreal mountains	–23.8	0.42	3.44	0.42	9
Pacific coastal mountains	–23.3	0.61	2.8	0.82	19
Boreal	–22.8	0.63	3.1	0.41	89
Arctic	–22.3	0.53	3.5	0.14	3

Note: The mean $\delta^{13}C$ values represent carbon values for bears that eat little meat in these ecosystems. $\delta^{15}N$ values are given to demonstrate the potential variation in meat consumption among bears in each sample group.

isotope ratio of plant foods eaten by bears, $\delta^{15}N_{terr}$ is the average isotope ratio of terrestrial animal foods eaten by bears, and $\delta^{15}N_{salmon}$ is the average isotope ratio for salmon (Table 1). We determined $\delta^{15}N_{plant}$ by inserting 2.85 for $\delta^{15}N_{bear}$ into eq. 2 above and setting T to zero. This value was the mean $\delta^{15}N_{bear}$ for the four bear populations described above that are known to eat little terrestrial meat. We did not use the absolute minimum stable carbon or nitrogen isotope ratios to calculate plant baselines because we did not want to base our endpoint derivations on single extreme values.

When the population was known to have four major diet components, we used the IsoSource model approach advocated by Phillips and Gregg (2003) (method 7). This approach was used for 12 populations in central British Columbia that were known or presumed to eat spawning kokanee, Pacific salmon, plants, and terrestrial meat.

To increase the accuracy of our results, especially when using method 7, which often resulted in a wide range of pos-

sible solutions, we assumed a diet component fraction was zero when the mean estimate was <1% and used a simpler analytical method. Our calculations of diet fractions are based on generalized food baselines and should not be interpreted as accurate measures of assimilated carbon or nitrogen; we present relative measures of protein in the diet for comparison across the continental range of grizzly bears. More accurate measures of diet can be developed using regional isotopic baselines and with the addition of further diet components and isotope markers (e.g., Felicetti et al. 2003*b*; Ben-David et al. 2004).

Mapping diet

We mapped the geographic center of each population as a point in a geographic information system and used the triangular irregular network (TIN) procedure to interpolate a surface of mean diet components across western North America. We added six dummy points to the data set to in-

crease the size of the interpolated area such that the surface reached the edge of the continent. Dummy points were added only within the area of a population unit for which we had isotope data, hence these points essentially extended the diet measures to the edge of an area where diet had been measured. The TIN surface is based on simple linear relationships among three adjacent points and does not smooth or detect spatial trend. Smoothed maps are cleaner and may at times be more accurate, but we felt our data were too heterogeneously dispersed for us to use an algebraic smoothing procedure. In addition, TINs clearly demonstrate spatial weaknesses or incongruities in the point data.

Body size and diet

Skull size and specimen age have been recorded by government inspectors for almost all bears killed in British Columbia since 1975. Skulls were measured when unskinned, fresh skinned, or skinned, boiled, and cleaned. Based on data from the entire data set ($n = 3840$ males and 2018 females), which combines all ages except cubs, boiled and cleaned skulls averaged 5 mm shorter than fresh skinned skulls for both males and females. Unskinned skulls averaged 11 and 13 mm longer than fresh skinned skulls for males and females, respectively. Width of boiled skulls averaged 5 mm less for males and 3 mm less for females than width of fresh skinned skulls. Unskinned skulls averaged 9 and 11 mm wider than fresh skinned skulls for males and females, respectively. We used these means to estimate a fresh skinned skull measurement for boiled and unskinned skulls. Age was measured using the cementum annuli method and included a fraction of the year based on the month the bear was killed. Most bears were killed in spring or fall.

Growth of skull size was described by fitting the skull size measurement (length or width) to age with a Gompertz growth equation (Zullinger et al. 1984) through a three-parameter, nonlinear model:

[3] $\qquad L = Ae^{-e^{-K(Y-I)}}$

where Y is age in years, L is skull length or width in millimetres, A is asymptotic skull length or width, K is a growth constant (age^{-1}), and I is the inflection point. We used STATISTICA® Version 6.0 (StatSoft Inc., Tulsa, Oklahoma) to fit a model with three unknowns (K, I, and A) using iteration. We used data from 255 hunter-killed bears from British Columbia (169 males, 86 females) for which we had both diet and size measures to determine the effects of age and diet on body size. We excluded cubs and yearlings and seven outliers that appeared to have mistakes in the age, sex, or size data. Even though the Gompertz growth function was a biologically meaningful size at age relationship, a logistic relationship ($l = a + b\log(age)$) also represented a statistical fit to the data (e.g., for male width, $r_{Gompertz} = 0.74$ vs. $r_{logistic} = 0.74$), meaning that we could use log(age) to linearize skull length and width measures and carry out multiple linear regression analysis using log(age) as an independent variable to account for the influence of age on size. Linear regression was used to examine the relationship between diet and size; salmon and terrestrial meat diet fractions, log(age), and sex were included in the regressions. Salmon and kokanee diet fractions were summed and inserted in place of salmon to assess whether kokanee helped explain growth patterns.

We used simple bivariate regression to determine the relationship between diet and age. In these cases we excluded samples where the diet fraction of interest was zero; we assumed bears with a diet fraction of zero did not have access to the food type, although we acknowledge that this assumption is probably not always true. Residuals were normally distributed for all regressions. We used partial correlations to compare the fit of individual variables in the regression (Tabachnick and Fidell 1996).

Results

Isotopic signatures

$\delta^{13}C$ and $\delta^{15}N$ values were not linearly related (Fig. 1). There is modest variation in $\delta^{13}C$ among most bears with $\delta^{15}N$ values below 5‰, suggesting that bears that eat mostly plants have similar carbon signatures. But some bears with no access to salmon have increased $\delta^{13}C$ values similar to those seen for bears that eat salmon. Bears from the central Arctic in particular show enriched $\delta^{13}C$ values (Fig. 1). Other non-salmon-eating bears with enriched $\delta^{13}C$ values were usually from northern portions of the continent, where ungulate prey species have higher $\delta^{13}C$ values than prey further south (Table 1). Bears with moderate $\delta^{15}N$ values and low $\delta^{13}C$ values were consuming kokanee.

In general, mean carbon and nitrogen isotope ratios of populations were linearly related, which resulted in long, thin Euclidean spaces in mixing diagrams when plants, terrestrial meat, and salmon were potential diet components (Fig. S1[2]). The power to assign terrestrial meat was poor in these cases because there was no clear separation of end members. Kokanee had a unique signature relative to other food classes, which gave good power to assign a diet fraction for this food.

Diet

In coastal areas, where bears eat mostly salmon, males and females often have similar isotopic signatures (Table S1[2]). Where salmon is a smaller portion of the diet, females often eat less salmon than males, and where salmon is a much smaller part of the diet, females generally consume much less salmon than males. Males often had the highest individual $\delta^{15}N$ values in any given study area.

Salmon was detected in the diet of bears as far north as Kotzebue Sound. The highest salmon diet fractions were on the Alaska Peninsula and parts of the mainland in southeast Alaska and on the north coast of British Columbia. Bears in Owikeno Sound and Glacier Bay, Alaska, had lower salmon diet fractions than bears in all other areas of the Pacific coast. Salmon isotopic signals were rarely detected in the interior of the continent. The highest signals were detected in the Quesnel Lake and Wells Gray Park regions of central British Columbia (Fig. 2; digital map data are in Supplementary material[2]). Enriched $\delta^{13}C$ signals in bears from the central Arctic generated marine components comprising >50% of the diet, which is not supported by fieldwork (Gau et al. 2002; MacHutchon and Wellwood 2003 and citations therein). Therefore, we excluded the salmon endpoint from Arctic mixing models, although this may have biased other diet estimates. Hence, our analysis does not examine the potential for Arctic bears to feed on marine foods such as ana-

Fig. 1. Stable isotope ratios in guard hair of grizzly bears (*Ursus arctos*) from Alaska, Yukon, Northwest Territories, Nunavut, British Columbia, Alberta, and Montana. ●, data from bears that had no access to salmon; △, data from bears from treeless areas of Northwest Territories and Nunavut; ■, data from bears that may have had access to salmon.
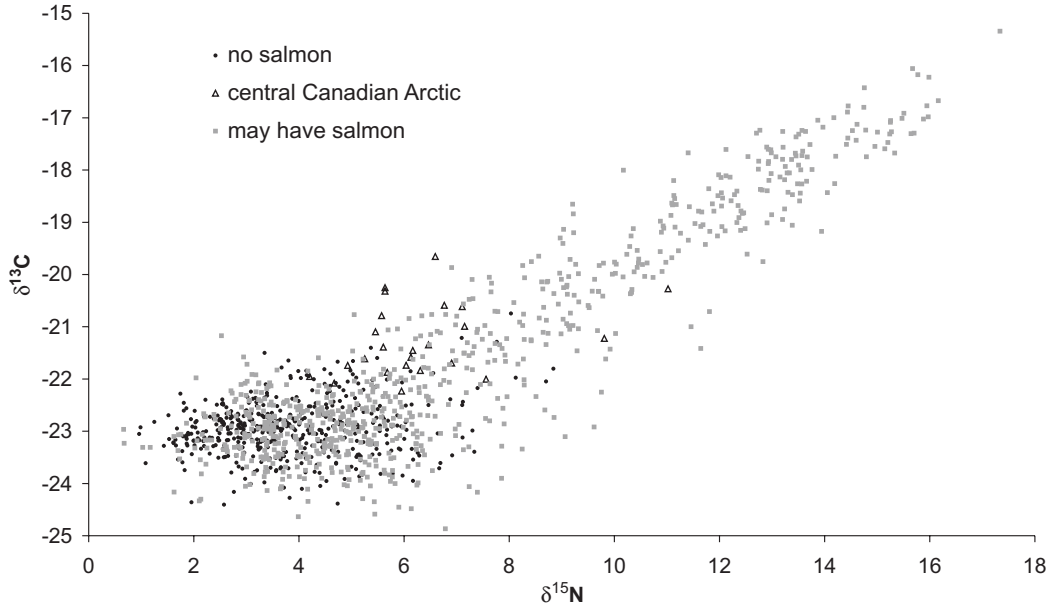
Fig. 2. Interpolation of the amount of salmon in the diet of grizzly bears across North America. The map is based on 81 data points (circles; Table 3) and 6 redundant points added to the edge of some population areas to expand the final map size. We used the triangulated irregular network procedure in ArcView® 3.2 (Environmental Systems Research Institute, Inc., Redlands, California) to derive the map.
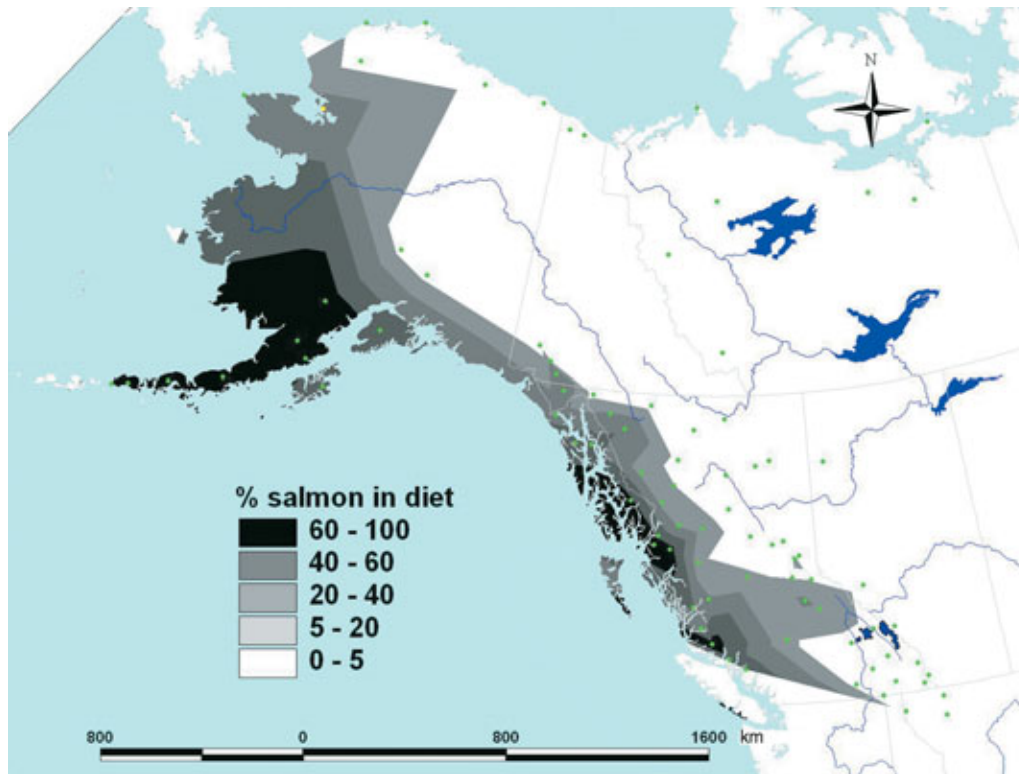

dromous Arctic char (*Salvelinus alpinus* (L., 1758)), whales, or seals.

In Arctic areas, where barren-ground caribou were available and terrestrial meat consumption was higher than elsewhere, nitrogen signatures were similar between sexes. Nitrogen signatures were also similar between sexes in three

Fig. 3. Interpolation of the amount of terrestrially derived meat in the diet of grizzly bears across North America. The map is based on 81 data points (circles; Table 3) and 6 redundant points added to the edge of some population areas to expand the final map size. We used the triangulated irregular network procedure in ArcView® 3.2 (Environmental Systems Research Institute, Inc.) to derive the map.
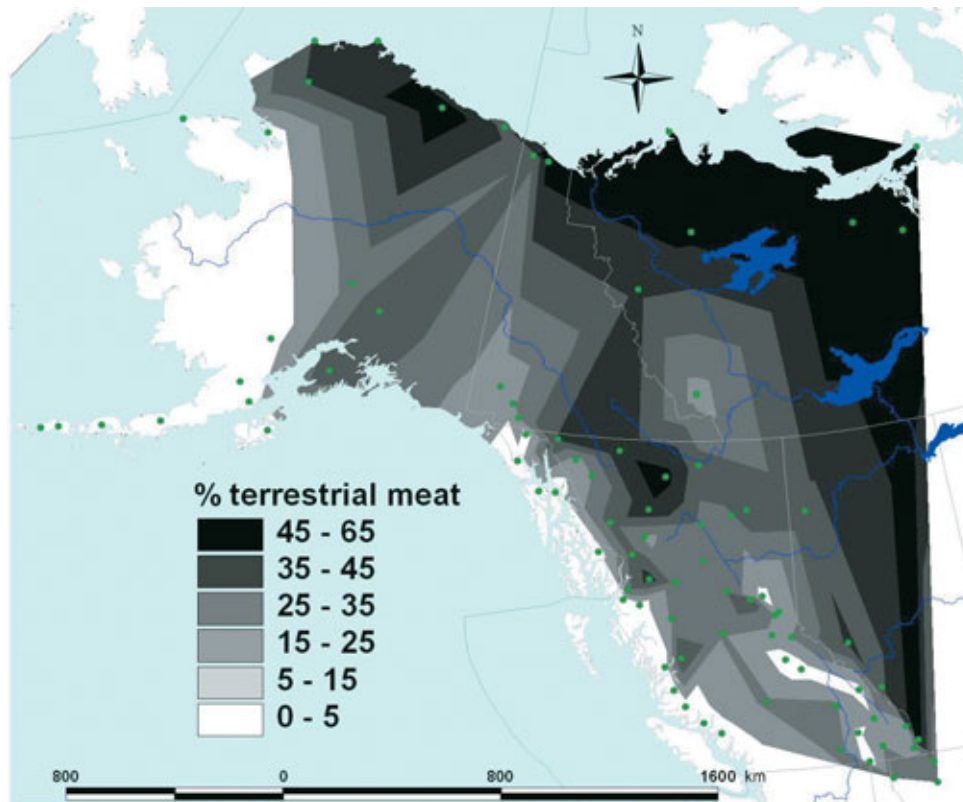
boreal populations in northern British Columbia (Cassiar, Spatsizi, and Muskwa), where terrestrial meat consumption contributed >40% of assimilated nitrogen. Where terrestrial meat consumption was lower, males tended to have higher nitrogen signatures than females (Table S1[2]). Terrestrial meat consumption was near zero in the west slopes of the Rocky Mountains north to the Hart Ranges in east central British Columbia (Fig. 3; digital map data are in Supplementary material[2]). Dryer areas to the east and west showed measurable terrestrial meat consumption. Most boreal areas, such as the interior of northern British Columbia and Alaska, showed higher terrestrial meat consumption, although we sampled few populations from these areas. Arctic regions that supported barren-ground caribou consistently showed the highest terrestrial meat consumption.

Kokanee was a detectable part of the diet in many areas in central British Columbia. Average predicted contributions to assimilated carbon and nitrogen varied from 3% to 28% among populations, suggesting that kokanee provided an important contribution to the diet in some areas (Fig. S2[2]). Predicted contributions to diets of individual bears were as high as 36%.

Body size and diet

Skull lengths reached 95% of their asymptotic size at age 8 for males and age 5 for females; skull widths increased until 14 and 8 years for males and females, respectively (Fig. 4).

Diet fractions averaged 17% (SD = 27) for salmon, 5% (SD = 8) for kokanee, and 24% (SD = 21) for terrestrial meat for 255 hunter-killed bears from British Columbia. Skull length increased with increasing amounts of salmon and terrestrial meat in the diet ($F_{[4,250]} = 76.8$, $R^2 = 0.55$, $P < 0.001$), as did skull width ($F_{[4,249]} = 90.7$, $R^2 = 0.59$, $P < 0.001$). Adding kokanee to the salmon measure mildly improved the fit over salmon alone for skull length ($F_{[4,250]} = 80.3$, $R^2 = 0.56$, $P < 0.001$) and width ($F_{[4,249]} = 93.1$, $R^2 = 0.60$, $P < 0.001$). In all four above models the slope for salmon was 28%–71% greater than that for terrestrial meat, while the error of the slope estimate was 21%–22% greater for terrestrial meat. Further, partial correlations for salmon or fish were at least 2.5× larger than those for terrestrial meat. These data suggest that fish (largely salmon) influences size to a greater extent than terrestrial meat, but confidence intervals of the slopes for fish and meat overlapped in all four models above. Indeed, simpler models, where all three sources of meat were summed, fit the data as well as the above models for both length ($F_{[3,251]} = 105.2$, $R^2 = 0.56$, $P < 0.001$) and width ($F_{[3,250]} = 124.1$, $R^2 = 0.60$, $P < 0.001$; Fig. S3[2]).

Where salmon was >30% of the diet, the contribution of salmon to the diet increased with age for males, but where salmon was a smaller fraction of the diet, there appeared to be no relationship between diet and age for either sex (Fig. 5a). The amount of terrestrial meat in the diet did not change with age ($n = 73$ and 146, $P > 0.11$; Fig. 5b), while

Fig. 4. Mean skull size and 95% confidence intervals by age for hunter-killed grizzly bears from British Columbia, 1975–2005 (n_{males} = 3840, $n_{females}$ = 2018). We combined all ages >24 years for males and >21 years for females. Curves were generated with the raw data using a Gompertz growth equation; see Methods for details. To plot the graph, ages were rounded to the nearest whole number of years; hence, age depicts the number of summers each bear lived. Lines indicate the age when 95% of the asymptotic size was reached. Male skull length = $375e^{-e^{-0.273(Age-(-3.15))}}$ (R = 0.62), female skull length = $329e^{-e^{-0.383(Age-(-3.14))}}$ (R = 0.44), male skull width = $236e^{-e^{-0.170(Age-(-3.24))}}$ (R = 0.74), female skull width = $195e^{-e^{-0.244(Age-(-3.66))}}$ (R = 0.60).
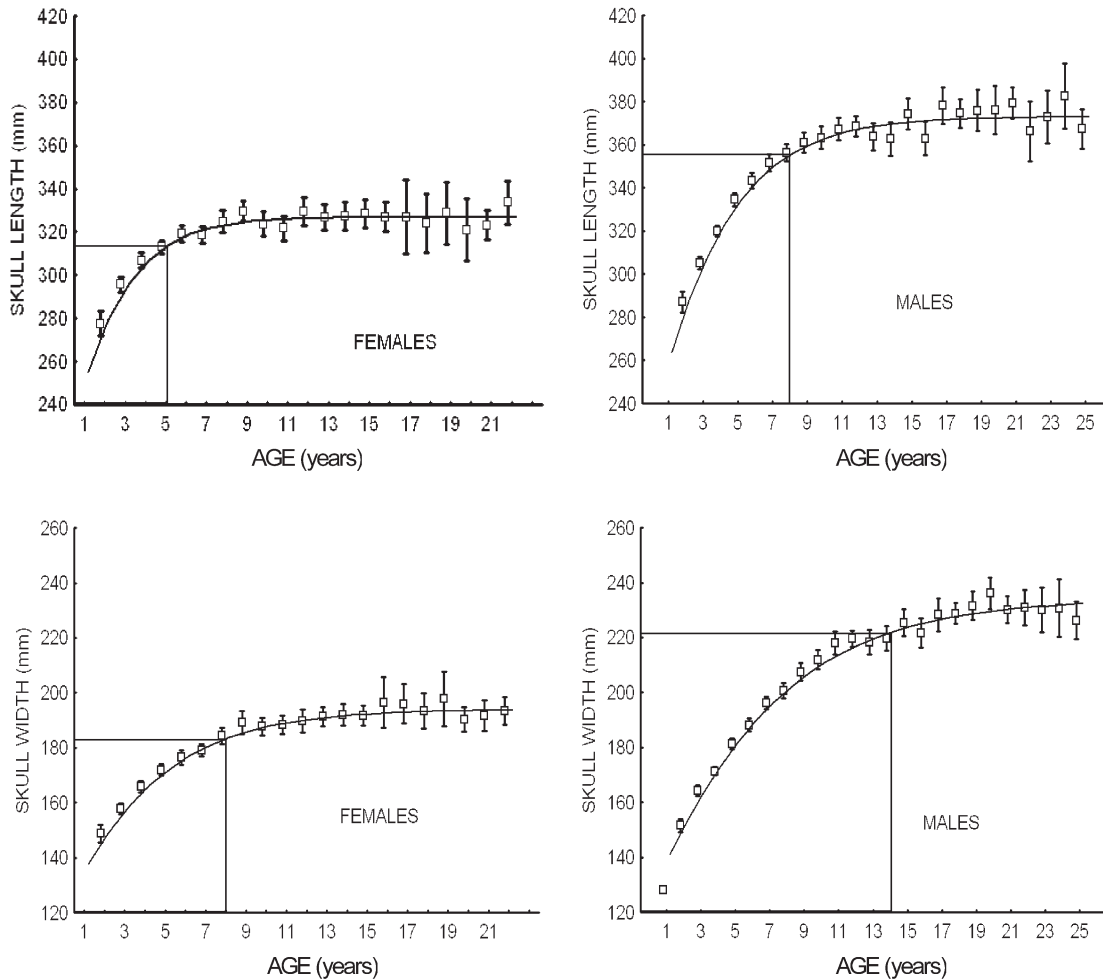
the amount of kokanee in the diet decreased with age for both males ($F_{[1,63]}$ = 3.5, R^2 = 0.05, n = 65, P = 0.07) and females ($F_{[1,29]}$ = 14.2, R^2 = 0.33, n = 31, P < 0.001; Fig. 5c).

Discussion

Salmon make major contributions to grizzly bear diet throughout the Pacific coast of North America (Hilderbrand et al. 1999a). In our study, salmon was <33% of the diet in only three coastal areas: Owikeno Sound in southwest British Columbia (Boulanger et al. 2004), Glacier Bay in southeast Alaska (Tania Lewis, US National Parks Service, Glacier Bay, Alaska), and Kotzebue Sound along the Bering Strait (Miller et al. 1997), and each of these areas had relatively few salmon available. The fact that males and females had similar salmon diet fractions in coastal areas suggests that salmon was abundant and dispersed enough to be available to most of the adult population, although some females may choose to avoid streams to minimize the risk of infanticide (Ben-David et al. 2004). The variance in salmon diet

fractions within sexes may indicate the degree to which males and females use the same streams (Nevin 2003; Gende and Quinn 2004) in response to both within-sex social interactions and competition between the sexes (Gende and Quinn 2004).

Female bears with cubs are hypothesized to avoid salmon streams to minimize the risk of infanticide from males (Ben-David et al. 2004). Admiralty and Chichagoff islands, where some females have already been shown to avoid salmon streams, were the only two coastal study areas where females consumed less salmon than males. But the data we present do not test the hypothesis well because most of our coastal data came from hunter-killed bears. Because hunters are prohibited from killing females accompanied by cubs, our sample may not accurately document female avoidance of salmon streams. Three coastal samples were drawn from live-captured bears, which presumably better reflect all females in the sample, and males and females had similar nitrogen signatures in all three areas. However, our sample sizes for females were 6–7 for these three areas, while the

Fig. 5. Relationship between grizzly bear age and (*a*) the proportion of the diet consisting of salmon, (*b*) the proportion of the diet consisting of terrestrial meat, and (*c*) the proportion of the diet consisting of kokanee. Diet was calculated based on isotope analysis of entire guard hairs and several different linear mixing models (see Methods). Only samples with salmon, meat, and kokanee diet fractions > 0 were included in (*a*), (*b*), and (*c*), respectively.

sample sizes for females from Admiralty and Chichagoff islands were 31–33. Thus, our samples were likely too small or biased to detect females that had chosen to avoid salmon streams to protect their cubs.

In areas where salmon was <33% of the diet, males regularly had higher nitrogen signatures than females, which suggests that resources are less widespread or abundant and that males are able to monopolize the salmon resource (see Gende and Quinn 2004 for a review of the influence of social dominance on foraging). In contrast, following a major decline in salmon returns in Owikeno Sound, bears consumed less salmon than elsewhere along the coast, but both sexes had similar nitrogen signatures.

The pattern of consumption of terrestrial meat was similar between sexes. In most areas of the Rocky Mountain west slopes, ungulates are not abundant (Shackleton 1999); nitrogen signatures were similar between the sexes and consistently suggested that little terrestrial meat was consumed (this study, Hobson et al. 2000). Males are likely unable to monopolize terrestrial meat resources in interior areas except perhaps where gut piles from hunter-killed ungulates are very common. The pattern of terrestrial meat consumption between sexes would suggest that at high ungulate densities, males and females encounter and exploit ungulates at similar rates. At lower ungulate densities the resource is more clumped and males spend more time actively hunting, are more likely to be able to defend carcasses until they are consumed, or encounter ungulates more often than females because of their larger home ranges. Other authors have shown that male grizzly bears consume the greater portion of a meat resource that occurs in relatively small patches. For example, male bears consumed more spawning cutthroat trout (*Oncorhynchus clarkii bouvieri* (Jordan and Gilbert, 1883)) than females, and spawning fish are confined to a portion of the small streams in the Greater Yellowstone Ecosystem (Felicetti et al. 2004). Jacoby et al. (1999) showed that male bears typically had higher meat consumption than females in areas of the continental Midwestern United States; these bears fed on presumably predated ungulates and scavenged road-killed ungulates. In contrast, bears that fed heavily on cattle had similar terrestrial meat intakes among sex and age classes.

The highest terrestrial meat diet fractions were consumed by grizzly bears in Arctic areas where caribou were abundant. Similarly, moose were abundant in areas of Alaska and British Columbia where terrestrial meat diet fractions were also high (Miller et al. 1997; Hilderbrand et al. 1999*b*; Shackleton 1999). Ungulates are abundant along the Rocky Mountain east slopes and in parts of the central interior of British Columbia, and terrestrial meat fractions were modest to high in these areas. Terrestrial meat fractions were lowest
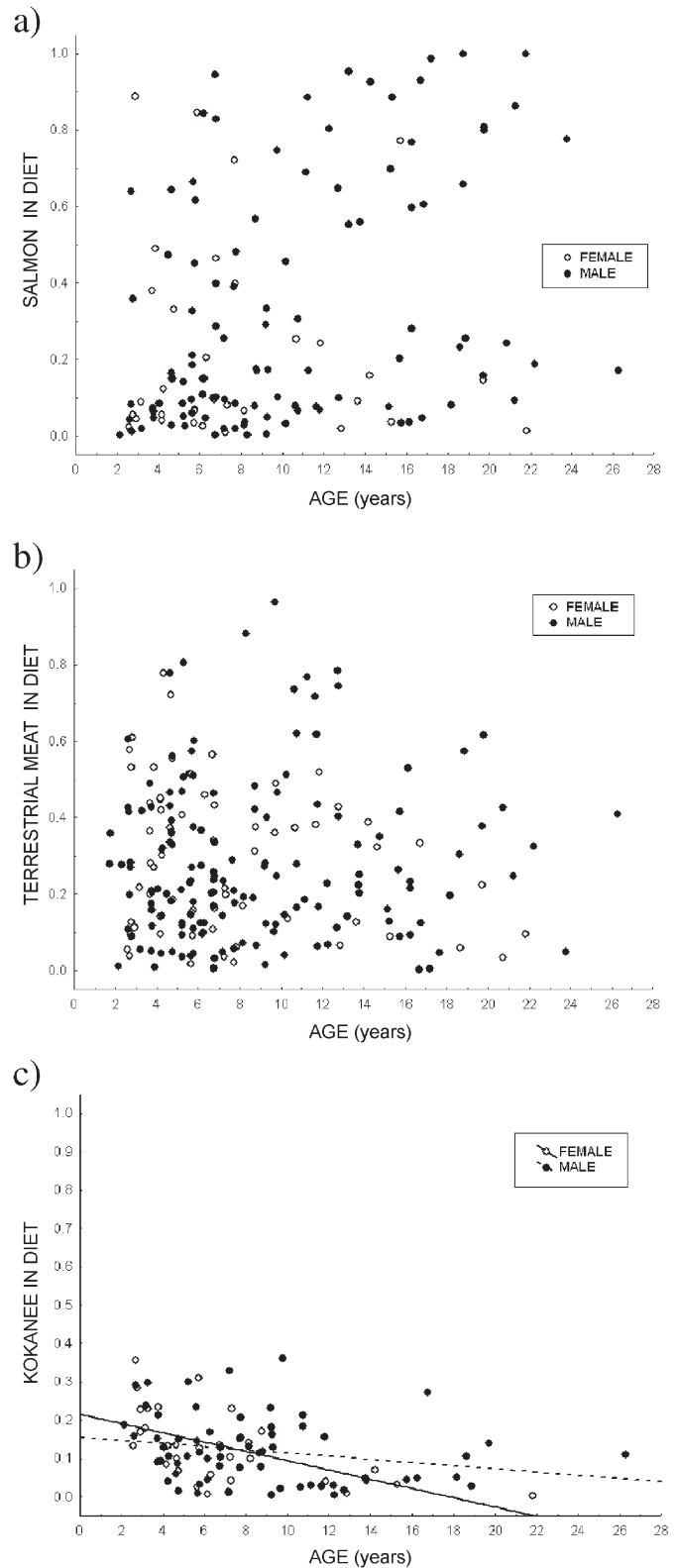
in wet areas, where forests are dense and ungulates are not abundant. Our data suggest a weak negative relationship between climate moisture and the fraction of the diet that consists of terrestrial meat. The functional relationship is probably between bears and ungulates, with ungulate num-

bers being higher where there is less snow (Kelsall and Telfer 1973; Crete 1976; Thomas and Toweill 1982).

Kokanee are sporadically abundant in parts of interior British Columbia and appear to be important contributors to diet in some areas. Diet estimates are based on three kokanee samples from central British Columbia; if kokanee isotope ratios are more similar to published data from Colorado (Johnson et al. 2002), then kokanee diet fractions may be overestimated by as much as 100%. Simulations using endpoints from Johnson et al. (2002) suggest that salmon diet fractions were little influenced by inaccuracy in the kokanee endpoint, whereas terrestrial meat would have been slightly underestimated. Kokanee were important to certain individual bears: 75 of 272 bears for which we calculated individual diet had >5% kokanee in the diet and 10 bears were predicted to consume >25% kokanee. Kokanee were consumed in some areas where anadromous salmon were also available, and kokanee spawn at similar times to chum (*Oncorhynchus keta* (Walbaum in Artedi, 1792)) and sockeye (*O. nerka*) but are much smaller than anadromous salmon. Presumably some bears chose to fish kokanee rather than move to salmon streams. Our data suggest that younger bears fished kokanee (Fig. 5*c*) and then, when they got older and larger, caught more salmon (Fig. 5*a*). Spawning cutthroat trout appear to be important food for a few individual male bears in the Greater Yellowstone Ecosystem but are not currently a significant resource at the population scale (Felicetti et al. 2004).

What is the functional role of diet in bear population dynamics? Bears that eat meat grow larger, and size is related to population density, productivity, and other vital population rates (Stringham 1990; Hilderbrand et al. 1999*a*; Ferguson and McLoughlin 2000). The amount of meat consumed is related to both skull length, which is an index of subadult nutrition and growth, and skull width, which indexes growth during the subadult and adult phases of a bear's life. However, the influence of terrestrial meat on body size was only weakly supported by our data.

Rausch (1963) suggested a clinal variation in bear size across North America based on topographical gradients but gave no functional explanation for that trend. His data (Fig. 2 in Rausch 1963) also support our evidence that bear size is related to the amount of salmon in the diet: bear populations he studied that had no access to salmon had mean skull lengths of 324–349 mm; those with some access to salmon had skull lengths ranging from 346 to 366 mm; and coastal populations with access to abundant salmon had skull lengths ranging from 361 to 440 mm. Further, Rausch (1963) suggested a clinal increase in size among coastal populations from south to northwest, which roughly follows our predicted increase in salmon diet fraction for these populations. He further suggested clines in size for interior populations, which are explained by the presence of salmon in south central Alaska and the Kotzebue Sound region of northwest Alaska.

Nutritional ecology studies suggest that bears that eat meat in spring tend to add lean body mass, whereas in fall excess protein is converted to fat (Hilderbrand et al. 1999*b*; Felicetti et al. 2003*a*). The season in which terrestrial meat is consumed likely varies among individuals and areas to a greater extent than the season in which salmon is consumed. In boreal areas, where bears feed largely on moose, calves are the main prey and are killed in spring (Ballard et al. 1981; Gasaway et al. 1992). In areas where hunting is common, gut piles may be a large portion of ingested meat (Haroldson et al. 2004), and these are consumed in fall except in the Arctic, where hunting often occurs in spring and late summer. Bears in the Arctic consistently showed the highest meat fractions in their diet, and presumably caribou are consumed during all seasons (Reynolds and Garner 1987; Gau et al. 2002; MacHutchon and Wellwood 2003). The variation in the season of terrestrial meat use may generate greater variation in the relationship between meat in the diet and bear size at the continental scale.

Arctic-dwelling bears are not larger than other bears that eat much less meat (Rausch 1963; Kingsley et al. 1988); indeed, some populations appear measurably smaller (Ferguson and McLoughlin 2000; Schwartz et al. 2003) and densities are very low. Perhaps bears without access to salmon are smaller because of the high variation in ungulate abundance in space and time, which demands that bears never get so large that their size precludes their ability to gain and maintain mass feeding on vegetation. Alternatively, vegetation quality may also explain a portion of the variation in grizzly bear size across their range (Robbins et al. 2004).

We conclude that the amount of salmon in the diet is functionally related to the size of individual bears but that there is a weaker relationship between size and the amount of terrestrial meat in the diet. Plant quality also influences body size in bears (Robbins et al. 2004). Ultimately, the amount of salmon or meat in the diet influences population density at the continental scale (Hilderbrand et al. 1999*a*), and perhaps at finer scales as well. Density was higher in two western Arctic grizzly bear populations with access to abundant caribou than in a population with no such access (Reynolds and Garner 1987).

There are methodological limitations that may influence the above conclusions. Guard hair indexes diet for a single year, and the relationship between size and salmon fraction would suggest that yearly measures of salmon assimilation roughly index the importance of salmon for the life of the bear. Consumption of terrestrial meat may be more variable among years and hence the signal derived during a single year may not index lifetime consumption of meat well. This possibility seems slight, at the population level at least, because the trend in meat consumption was consistent across the continent; the signal from guard hairs generally documented that bears ate more meat where ungulates were more abundant. Also, our results are generally consistent with diet estimates made using other methods (Reynolds and Garner 1987; McLellan and Hovey 1995; Mattson 1997; Gau et al. 2002; MacHutchon and Wellwood 2003 and citations therein), although, as expected, isotope analysis suggested that meat is a larger portion of assimilated protein than traditional analysis methods indicate.

Our analysis of bear size and diet provides several insights regarding bear life history. The observation that the salmon diet fraction increases with age for males but not necessarily for females emphasizes the difference in life-history constraints between the sexes. Males grow larger

with age, which allows them to dominate resources both within and among species. The much larger body size of males reduces their ability to gain and maintain mass feeding on vegetation (Welch et al. 1997; Rode et al. 2001). This limitation may synergistically encourage male bears to monopolize salmon resources. In contrast, females are smaller and are better able to maintain their body mass on vegetation alone, and some females even elect to forage away from salmon concentrations, presumably to reduce the risk of infanticide by males (Ben-David et al. 1994). Choosing to avoid spawning areas does not appear to be a lifelong strategy because females that elect not to feed on salmon for a single year are not smaller than those that do (Ben-David et al. 2004). Our limited data suggest considerable variation in yearly consumption of salmon among adult female bears (compare the SD of mean isotope values between sexes in Table S1[2]), which is consistent with a portion of females avoiding salmon feeding areas. As suggested earlier, kokanee may be used more by younger bears as an alternative to fishing for salmon where conflict with larger and older bears is more likely.

Our data on age and skull size were collected throughout British Columbia from areas with large differences in bear density and resource availability, but our conclusions appear to be general to bears across North America. Skull dimensions of bears from both the Arctic (Kingsley et al. 1988) and the Alaska Peninsula (Glenn 1980) also showed that bear skull length asymptotes at around 8 years for males and 5 years for females and that width continues to grow throughout most of the bear's life.

How accurate are our predictions of diet? The distribution of our data is spotty, and the north and south ends of the range are least covered. Many populations in the south are not hunted, so fewer samples were collected there. We had few samples north of the Alaska Peninsula, so our maps are based on large extrapolations north of Anchorage in Alaska. The coastal portion of Alaska north of Bristol Bay was mapped using data from two sample populations near Nome and Noatak. Our map indexes salmon consumption only crudely in this area. Similarly, inter-population variation in meat consumption is poorly captured throughout the north by our map, given the paucity of samples we had for such a large area.

The salmon diet fraction for one study area was likely biased low. For the Susitna Valley area of interior Alaska we had data only from females, and because this was an area with moderate terrestrial meat consumption and low salmon consumption, males likely had higher signatures than females. Our salmon diet fraction was estimated to be zero but the field biologists observed considerable use of a salmon spawning area in a portion of the study area (Miller et al. 1997). Therefore, the estimate for the Susitna Valley area is likely biased low owing to the lack of males in the sample. We had data for a single sex in nine other areas, including the Kenai Peninsula, but the differences in diet between sexes were likely small in these areas (Hilderbrand et al. 1999b).

Using local plant and animal endpoints, Hobson et al. (2000) predicted very small meat fractions for 46% of male and 18% of female bears and no meat in the diet of the re-

maining bears in their sample from the Rocky Mountain west slopes of British Columbia, whereas our general model predicted no meat in the diet of that population. This result was expected because we used the carbon and nitrogen signatures from four study areas in this region to calculate the plant endpoints. In essence, this set the terrestrial meat consumption for these four areas to zero.

We used data from the same 12 populations studied by Hilderbrand et al. (1999a) and our salmon fractions were similar except on Admiralty Island, where our estimate was lower and more similar to results reported by Ben-David et al. (2004). Our estimates of terrestrial meat fractions were higher than those of Jacoby et al. (1999) and Hilderbrand et al. (1999a) in all areas except coastal regions, where salmon were abundant, because here we did not consider meat a possible diet source in our models (except for the Kenai Peninsula, where moose are more abundant than they are in other coastal areas; Hilderbrand et al. 1999b). Our assumption would appear reasonable because these authors found little evidence for use of terrestrial meat in coastal areas. Our estimates of terrestrial meat consumption in interior areas are higher than the estimates of these earlier authors because we used a lower plant baseline that was specific to bears.

Guard hairs provide a reasonable integration of yearly diet because they are grown over a period of up to 5 months (Felicetti et al. 2003b). In addition, they contain both protein and a stable inner core of lipids; hence, hair should integrate the assimilation of protein, carbohydrates, and fat. Hair can be collected noninvasively across broad areas, making large-scale collections of hair much easier than collections of blood or other tissue. We have shown that variation in repeated measures of stable isotope ratios among different hairs is not trivial but neither is it large enough to mask continental-scale variation in diet. Future researchers may minimize sample variance by analyzing several hairs from the same bear (Ben-David et al. (2004) analyzed at least two from each bear) or by using only spring- or fall-collected hair so that hair growth is complete and documents the entire year's diet (as in Felicetti et al. 2004).

The larger problems in our analyses likely revolve around fractionation, especially of carbon, and the derivation of endpoints. Fractionation studies have tended to compare blood components with diet because blood components equilibrate to the diet faster than an entire guard hair does (Hilderbrand et al. 1996; Felicetti et al. 2003b) and are therefore easier to study in captive animals. But carbon shows different fractionation in hair than in plasma or blood (Hobson et al. 1996; Roth and Hobson 2000; Sponheimer et al. 2003) and the fractionation relationship between diet and consumer $\delta^{13}C$ values is not simple (Hilderbrand et al. 1996; Ben-David and Schell 2001; Felicetti et al. 2003b; Ben-David et al. 2004). Felicetti et al. (2003b) argued against using carbon isotopes to make inferences about diet because of the high variation in fractionation resulting from the complexities of carbon metabolism. Clearly, more controlled studies of carbon fractionation in bear hair are needed.

Fractionation of nitrogen appears to be similar in hair and other tissues (Hobson et al. 1996; Roth and Hobson 2000). The $\delta^{15}N$ fractionation curve presented by Felicetti et al.

Table 3. Major diet components, diet calculation method, weighted isotopic means, weighting method, and period of sample collection for grizzly bear populations across North America.

Study area	Latitude	Longitude	Proportion of diet				Calculation method[a]	δ13C (‰)	δ15N (‰)	Weighting method[b]	Year(s)
			Plants	Salmon	Meat	Kokanee					
Admiralty	58.02	−134.44	0.52	0.48			1	−20.2	9.3	1	1982–2000
Alaska GMU 10	54.75	−164.00	0.21	0.79			1	−17.6	13.4	5	2003–2004
Alaska GMU 23	66.70	−161.60	0.72	0.28			1	−21.9	6.5	1	2003–2004
Alaska GMU 9B	60.50	−154.80	0.29	0.71			1	−17.7	12.4	3	2003–2004
Alaska GMU 9C	58.80	−155.50	0.27	0.73			1	−18.0	12.6	3	2003–2004
Alaska GMU 9D	55.50	−161.90	0.27	0.73			1	−17.7	12.6	1	2003–2004
Alberta	57.67	−122.55	0.67		0.33		4	−23.2	4.2	1	2000–2003
Arctic National Wildlife Refuge	69.86	−142.92	0.68		0.32		3	−21.9	4.5	4	Before 1998
Babine	55.30	−126.90	0.54	0.09	0.21	0.16	7	−22.6	6.2	1	1995–2003
Banff	51.40	−115.86	0.67		0.33		2		4.6	1	1994–2002
Bathurst Inlet	66.20	−109.00	0.40		0.60		3	−21.0	5.9	1	1997
Black Lake	56.53	−158.94	0.18	0.82			1	−19.4	13.8	4	Before 1998
Bowron	53.50	−121.50	0.70	0.04	0.11	0.15	7	−23.2	5.1	1	2002
Bulkley Lakes	54.10	−127.10	0.63	0.06	0.16	0.15	7	−22.9	5.6	1	1995–2003
Cabinet–Yahk	48.36	−115.92	0.79		0.21		2		4.0	1	1977–1996
Cassiar	59.60	−130.60	0.57		0.43		4	−22.9	4.7	1	1995–2003
Central Purcell	50.40	−116.50	0.93		0.07		2	−22.6	3.2	1	1998
Central Selkirk	50.00	−117.40	0.97		0.03		2	−22.9	3.0	1	1996
Chichagoff	58.00	−135.50	0.46	0.54			1	−20.0	10.1	1	2002–2003
Columbia Mountains	51.41	−117.07	1.00		0.00		2	−23.2	2.5	1	1994–1998
Cranberry	55.40	−128.40	0.30	0.17	0.40	0.13	7	−21.5	7.9	1	1995–2003
Denali	63.21	−150.98	0.82		0.18		4	−23.1	3.6	4	Before 1998
Edziza – Lower Stikine	57.20	−130.90	0.59	0.12	0.29		5	−22.4	5.7	1	1995–2003
Elk Valley	50.00	−114.90	0.89		0.11		2	−22.7	3.4	1	1997
Finlay–Ospika	57.20	−125.40	0.68		0.22	0.10	6	−22.9	4.5	1	1995–2003
Flathead	49.25	−114.70	0.88		0.12		2	−22.8	3.5	1	1997
Glacier Bay	58.89	−137.07	0.69	0.31			1	−20.4	7.0	1	2002–2003
Glacier National Park, Montana	48.70	−113.80	0.79		0.21		2		3.9	1	1967–1996
Granby	49.50	−118.40	0.77		0.18	0.05	6	−23.1	4.2	1	1998
Herrick	54.24	−121.00	0.93		0.07		2	−23.0	3.2	1	1995–2003
Hinton	53.00	−117.35	0.63		0.37		2	−22.6	4.9	1	1999
Hyland	59.20	−125.50	0.71		0.29		4	−22.8	4.1	1	1995–2003
Ivvavik	69.10	−139.90	0.74		0.26		3	−22.4	4.2	1	1993–1995
Katmai	58.34	−154.50	0.37	0.63			1	−19.8	11.3	4	Before 1998
Kenai	60.23	−150.42	0.12	0.56	0.32		5	−19.9	12.1	4	Before 1998
Khutzeymateen	54.68	−129.86	0.22	0.78			1	−16.4	13.3	1	1989–1991
Kingcome–Wakeman	51.20	−126.26	0.31	0.69			1	−18.9	12.0	1	1995–2003
Kluane Park Central	60.74	−138.00	0.86		0.14		4	−22.5	3.4	1	2003

Table 3 (*continued*).

Study area	Latitude	Longitude	Proportion of diet				Calculation method[a]	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Weighting method[b]	Year(s)
			Plants	Salmon	Meat	Kokanee					
Kluane Park North	61.20	−139.00	0.91		0.09		4	−22.3	3.2	1	2003
Kluane Park South	60.30	−137.50	0.47	0.39	0.14		5	−20.9	8.1	1	2003
Kugluktuk	66.80	−112.80	0.39		0.61		3	−21.5	6.0	1	2004–2005
Lower Nass	55.00	−129.65	0.17	0.54	0.22	0.07	7	−19.7	11.6	1	2002–2003
MacGregor	54.14	−121.27	0.79	0.06	0.14		6	−22.5	4.4	1	1995–2003
Mackenzie Mountains	65.00	−130.00	0.63		0.37		4	−22.3	4.4	3	1995–2003
Mid Coast	52.50	−127.40	0.58	0.42			1	−20.3	8.4	1	1995–2003
Mid Susitna	62.65	−148.48	0.66		0.34		4	−21.5	4.3	4	Before 1998
Muskwa	58.80	−127.60	0.51		0.49		4	−22.5	4.9	1	1995–2003
Nahanni	61.53	−125.61	0.89		0.11		4	−22.7	3.3	1	2001–2003
Nation	55.00	−123.94	0.50		0.25	0.26	6	−23.7	5.9	1	2003
North coast	54.54	−128.90	0.33	0.67			1	−19.2	11.8	1	1995–2003
Northwest Alberta	57.50	−119.00	0.68		0.32		4	−23.3	4.2	1	1995–2003
Omineca	56.00	−125.25	0.62		0.23	0.15	6	−23.2	5.0	1	1995–2003
Owikeno	51.75	−126.90	0.71	0.29			1	−21.5	6.8	1	1998–1999
Parsnip Mountains	54.80	−121.90	0.98		0.02		2	−23.2	2.9	1	1995–2003
Parsnip Plateau	54.70	−122.60	0.68		0.32		2	−23.6	4.6	1	1995–2003
Prudhoe Bay	69.91	−148.85	0.48		0.52		3	−21.9	5.5	4	Before 1998
Quesnel Lake North	52.64	−120.84	0.68	0.23	0.00	0.08	7	−22.2	6.6	1	1995–2003
Robson	53.38	−120.40	0.75	0.04	0.15	0.06	7	−22.9	4.7	1	1995–2003
Rocky	57.50	−123.50	0.76		0.24		2	−22.7	4.1	1	1995–2003
Sahtu	67.00	−126.00	0.52		0.48		3	−21.2	5.3	3	1995–2003
Southeast mainland	56.20	−131.50	0.36	0.64			1	−19.1	11.4	1	1995–2003
Shuswap Monashee	51.00	−118.40	0.76		0.17	0.07	6	−23.3	4.3	1	1995–2003
South Purcells	49.46	−116.22	0.85		0.15		2	−22.9	3.6	1	1995–2003
South Selkirks	49.00	−116.99	1.00		0.00		2	−23.1	2.2	1	1996
Southern Interior Plateau	51.30	−122.00	0.74	0.06	0.17	0.03	7	−22.7	4.7	1	1995–2003
Spatsizi	57.70	−128.60	0.57		0.43		4	−23.1	4.7	1	1995–2003
Stewart	56.20	−129.50	0.41	0.12	0.29	0.18	7	−22.3	7.2	1	1995–2003
Southwest Alberta	49.50	−114.40	0.50		0.50		2	−22.5	5.5	1	1997
Swan mountains	48.00	−113.80	0.78		0.22		2	−22.9	4.0	1	2003
Taku	58.70	−132.30	0.48	0.37	0.15		5	−21.0	8.0	1	1995–2003
Tatshenshini	59.80	−136.80	0.70	0.30			1	−21.8	6.8	1	1995–2003
Tatuk	53.60	−124.20	0.49	0.06	0.16	0.28	7	−23.4	6.7	1	2001
Terror Lake	57.68	−152.74	0.49	0.51			1	−19.5	9.7	1	Before 1998
Toba Knight Bute	50.65	−125.30	0.47	0.53			1	−19.5c	9.9c	5	1995–2003
Tulsequah	59.19	−133.38	0.67	0.22	0.11		5	−21.8	5.9	1	2000
Tweedsmuir	52.80	−126.50	0.26	0.22	0.36	0.15	7	−21.4	8.6	1	1995–2003
Upper Skeena – Nass	56.80	−128.80	0.71	0.05	0.13	0.10	7	−22.8	5.0	1	1995–2003

Table 3 (concluded).

Study area	Latitude	Longitude	Proportion of diet				Calculation method[a]	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Weighting method[b]	Year(s)
			Plants	Salmon	Meat	Kokanee					
Wells Gray	52.30	–120.00	0.83	0.17	0.00		5	–22.1	4.3	1	1995–2003
Western Brooks Range	68.90	–160.65	0.64		0.36		3	–21.9	4.7	4	Before 1998
White Pass	59.80	–134.69	0.64		0.36		4	–22.6	4.3	1	1995–2003
Yukon north slope	69.00	–138.50	0.51		0.49		3	–23.3	5.4	1	2004

[a]1, used $\delta^{15}N$ to calculate salmon and plant components; 2, used $\delta^{15}N$ to calculate terrestrial temperate meat and plants; 3, used $\delta^{15}N$ to calculate terrestrial tundra meat and plants; 4, used $\delta^{15}N$ to calculate terrestrial boreal meat and plants; 5, used models in Hilderbrand et al. (1996); 6, used Isoerror with three diet components; 7, used Isosource with four diet components.

[b]1, females weighted as 60% and males as 40% for population mean; 3, no weighting by sex, used mean of all samples; 4, population mean based on females only; 5, population mean based on males only.

[c]Nevin (2003) presented isotope data from the Knight Inlet portion of this area: means for 1999–2001 were $\delta^{13}C = -20.9‰$ and $\delta^{15}N = 10.4‰$ ($n = 96$).

(2003*b*) shows good fit, and all other carnivore data (Hobson et al. 1996; Roth and Hobson 2000; Kurle 2002) that we plotted on this relationship also fit closely (and see Ben-David and Schell 2001: Fig. 3). The ultimate cause of the relationship between $\Delta\delta^{15}N$ and the $\delta^{15}N$ ratio of the diet may be based on diet quality, which is the percentage of absorbed protein that is retained (Robbins et al. 2005).

We derived isotopic endpoints for diet components from the literature and applied these over wide areas. For our derivation of plant endpoints we assumed that the mean diet of bears in four of our study areas included no meat. Further, we extrapolated this plant endpoint to the entire western portion of the continent. Generally, we have faith in the endpoints we derived from the literature because all except the kokanee endpoint were based on several measures. The endpoint for kokanee was the weakest because it was based on three different fish from a single area of interior British Columbia and was lower than values for kokanee from Colorado (Johnson et al. 2002). Any inaccuracy in this endpoint would likely have caused an overestimate of the importance of kokanee in the diet. The $\delta^{13}C$ endpoint we derived for plants was similar to the average cited for C_3 plants (Cerling and Harris 1999) and similar to the plant endpoint developed for the Kenai Peninsula using ungulates as surrogates for vegetarian bears (Jacoby et al. 1999). The similarity in carbon signatures among bears with low $\delta^{15}N$ values suggests that the carbon endpoint we developed for plants was robust. Neither the $\delta^{13}C$ values for vegetarian bears nor our derived ungulate endpoints suggest a decrease in $\delta^{13}C$ values with increasing latitude (Hobson et al. 1999). The ungulate endpoints we derived suggest an enrichment in ^{13}C with increasing latitude, although this may have more to do with differences in diet among regions and species than with a more fundamental continental-scale effect.

Perhaps the largest potential source of bias in our estimates of diet was the lack of separation of carbon and nitrogen endpoints for plants, ungulates, and salmon in Euclidean space (Fig. S1[2]). The distinctive carbon signature for kokanee generated clear separation of end members. The poor Euclidean separation of our diet groups meant we had to use simpler models than we preferred because isotopic signatures of bear hair were sometimes outside the mixing polygon. In most coastal areas we assumed terrestrial meat use was zero and we used a simple nitrogen mixing model to estimate the salmon and plant fractions. In the Arctic, enriched carbon ratios generated measurable salmon fractions and smaller terrestrial meat components (often zero). To avoid this untenable result, we set the salmon fraction to zero for all Arctic areas, which may have resulted in an overestimate of the terrestrial meat fraction. In six cases we could not make simplifying assumptions because bears were known to eat both ungulates and salmon; in these cases we used the hierarchical model of Hilderbrand et al. (1996) to estimate the three diet fractions. Also, we used the plant endpoint for the terrestrial carbon endpoint in these calculations because we had no way of knowing what the signature was for the plant and terrestrial meat components combined. This too may have resulted in an overestimate of the salmon component, although bias was likely small because the plant and animal endpoints were similar and much lower than that of salmon. Any overestimate of the salmon component

would have resulted in an underestimate of terrestrial meat consumption because the latter fraction is based on the fraction of the nitrogen signature that is unaccounted for by salmon (Hilderbrand et al. 1996). For these reasons we used Hilderbrand et al.'s methods only for the six cases when a simpler model was not tenable and the bear signature was outside the Euclidean space of the diet endpoints.

There is error associated with diet estimates regardless of the calculation method used. We did not emphasize precision because we were more interested in the spatial variation in diet. All our estimates of diet fractions (Table 3) should be treated as approximate.

Absorption and routing of specific molecules are general problems with the use of isotope analysis to assign diet (Phillips and Koch 2002; Robbins et al. 2002). Direct routing of fat from meat sources to stored lipids may cause underestimates of the importance of meat if the diet tissue analyzed contains little fat (or if the fat is removed). We suspect that this bias is reduced when hair is used instead of blood or muscle tissue because guard hair should integrate metabolite levels of both exogenous and endogenous carbon and nitrogen sources over most of the non-denning season, and hair is made up of stable portions of both protein and lipids.

Our diet data support Hilderbrand et al.'s (1999a) conclusion that meat is an important resource for grizzly bear populations. This conclusion was presumably based on the observation that salmon provide the majority of assimilated nutrients in coastal areas. We demonstrate that this observation is widespread and that terrestrial meat may provide the majority of assimilated resources in some ecosystems. We also provide a functional link between meat in the diet and fitness via body size. Bears can continue to grow well into their adult life, and the consumption of meat causes an increase in both subadult and adult body size. We conclude that spawning salmon are an important resource for grizzly bear populations, but evidence for the functional importance of terrestrial meat is inconclusive. We suggest that further work may demonstrate that salmon has a greater influence on body size and perhaps population-level parameters than terrestrial meat. Terrestrial meat sources are relatively secure but global climate change (Welch et al. 1998), hydroelectric dams (Hilderbrand et al. 1996), overfishing, and the alienation of spawning habitat all jeopardize salmon conservation (e.g., Boulanger et al. 2004) and, by extension, pose a threat to some of the highest density grizzly populations in North America (Miller et al. 1997; Hilderbrand et al. 2004).

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