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Temporal Variation in Stable Carbon and Nitrogen Isotopes of Grizzly Bear Guardhair and Underfur

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Abstract

*Animal diet investigations typically have been limited to stomach-content analysis, fecal analysis, or direct observation of foraging behavior. More recently researchers have used stable isotopes in tissues that develop during different time periods to examine the assimilated diet of mammals. Hair and bone tissues are used to examine annual and lifetime assimilated diets, whereas metabolically active tissues (e.g., blood, muscle, liver) reflect the assimilated diet over a period of days or months. Using hair tissue to examine assimilated diet at a finer temporal scale would be advantageous because samples can be collected without sacrifice or direct and continuous handling of an animal. We examined the possibility of using hair tissue to distinguish among seasonal assimilated diets of grizzly bears (*Ursus arctos*) by comparing the isotopic values of whole guardhair (annual assimilated diet), underfur (autumn assimilated diet), and replicate sections of guardhair for individuals within plateau and mountain environments in central British Columbia, Canada. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values differed between whole guardhair and underfur for male and female grizzly bears in the mountains and for $\delta^{15}N$ for female plateau bears. Consistent with our assumptions, isotopic values ($\delta^{15}N$ and $\delta^{13}C$) for the section of guardhair nearest the root overlapped with the underfur isotopic values for 7 of 8 bears. Overlap with subsequent sections was highly variable. Variation among replicates of guardhair sections within bears exceeded variation because of analytical error, indicating that current assumptions about hair growth may not be correct. The need to composite sample hair sections to meet minimum weight requirements precluded an examination of variation in isotopic values among individual hairs. Researchers examining the diets of grizzly bears should consider that differences can be detected between annual (whole guardhair) and autumn (underfur) assimilated diets, and there is potential to use sectioned guardhair to examine assimilated diet at a finer temporal scale; however, we suggest that controlled studies quantifying variation in hair tissue for bears on a constant diet and testing hair growth assumptions are integral to interpreting the temporal variation in assimilated diet using hair tissue.* (WILDLIFE SOCIETY BULLETIN 34(5):1320–1325; 2006)

Key words

carbon, diet analysis, grizzly bear, hair, nitrogen, stable isotope, technique, Ursus arctos.

Traditional methods of examining the diet of animals typically have been limited to stomach-content analysis, fecal analysis, and direct observation of foraging behavior (Hobson and Wassenaar 1999). Biases and limitations associated with traditional methods (McLellan and Hovey 1995) recently have led researchers to utilize stable isotopes to examine the assimilated diet of terrestrial mammals (Hilderbrand et al. 1996, Ben-David et al. 1997, Jacoby et al. 1999, Hobson et al. 2000, Robbins et al. 2004). Specifically in bears (*Ursus* spp.), the stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in different tissues have been used to determine the relative contributions of meat, plant, or marine (i.e., salmon) food sources in the assimilated diet (e.g., Hilderbrand et al. 1996, 1999*a*,*b*, Jacoby et al. 1999, Hobson et al. 2000, Ben-David et al. 2004), and provide insight into resource partitioning between bear species and sex (Jacoby et al. 1999, Hobson et al. 2000, Ben-David et al. 2004). These relationships are important because reproductive success, body size, and density of grizzly bears (*Ursus arctos*) are related to the amount of meat in the diet (Hilderbrand et al. 1999*b*).

Tissues used for stable isotope analysis (e.g., bone, muscle, hair) will reflect the assimilated diet during the period when the tissues were grown (Hilderbrand et al. 1996). Hair is commonly used to represent the average annual assimilated diet of grizzly bears (Hilderbrand et al. 1996, Jacoby et al. 1999, Hobson et al. 2000); however, quantifying assimilated diet using the isotopic value for sections of a guardhair may enable the examination of feeding history at a finer scale (e.g., Mizukami et al. 2005). The use of hair to examine assimilated diet at a finer temporal scale than a year is preferable to tissues commonly used (e.g., blood, liver) because hair samples can be collected at one time, without sacrifice or direct handling of the animal (e.g., barbed-wire snares), and large sample sizes can be obtained relatively cheaply.

In this study we examined the potential for evaluating seasonal assimilated diets of grizzly bears using sectioned guardhair by comparing isotope values in guardhairs to a similar structure (i.e., underfur), which is grown over a shorter period of time. If a whole guardhair represents the assimilated diet from May to October (Hilderbrand et al. 1996, Jacoby et al. 1999, Hobson et al. 2000, Felicetti et al. 2003), and variation is small along the length of a hair tissue for mammals on a constant diet (as reported in Hobson et al. 1996; but see figs. 1 and 2 in Hobson et al. 1996),

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differences in isotopic values among sections of guardhair should represent differences in assimilated diet during the time period that a section of hair was grown.

In order to examine seasonal assimilated diet using guardhair sections, it is important to know what time period a section of guardhair represents. We were particularly interested in the potential to distinguish between the annual and autumn assimilated diets because access to a constant meat source in autumn is correlated with higher grizzly bear densities (Hilderbrand et al. 1999*b*). We assumed that underfur is grown only in late summer and autumn, based on observations of underfur growth on shaved patches on the backs of captive bears (C. T. Robbins, Washington State University-Pullman, personal communication). Consequently, we compared the isotopic values between guardhair and underfur for individual grizzly bears to determine if isotopic values differed between annual and autumn periods and compared underfur and sections of guardhair to examine which section of guardhair best represented autumn. We used hair samples from grizzly bear populations whose food habits were known to vary among seasons but that had limited access to salmon (Ciarniello et al. 2002).

Study Area

We divided the central British Columbia, Canada, study area into 2 distinct topographical areas: mountains and plateau. The mountain region was characterized by steep mountains and rolling hills with highly variable terrain, ranging from approximately 670 to 2,370 m. Hybrid white spruce (*Picea glauca* × *engelmannii*) and subalpine fir (*Abies lasiocarpa*) were dominant at lower elevations, and Engelmann spruce (*Picea engelmannii*) replaced hybrid white spruce with increasing elevation. Subalpine fir became increasingly dominant at higher elevations, and the forest became more open, eventually turning into parkland containing stunted subalpine fir clumps interspersed with alpine meadows. Alpine areas occurred at elevations >1,500 m and were for the most part treeless. Potential food items for mountain bears included plants, berries, ants, rodents, and ungulates (Ciarniello et al. 2002).

The plateau region of the study area was characterized by flat terrain and rolling hills ranging from approximately 580 to 1,690 m. Forests in the plateau were dominated by hybrid white spruce, subalpine fir, and lodgepole pine (*Pinus contorta*), with occasional occurrences of black spruce (*Picea mariana*) in wetter regions. Potential food items for plateau bears included plants, berries, ants, rodents, ungulates, and domestic livestock (Ciarniello et al. 2002). Grizzly bears on the plateau also had access to several landfills.

Methods

Hair was removed directly from live-captured bears (Ciarniello et al. 2002) or from barbed wire put out to snare hair for a DNA mark–recapture study in 2001 (Mowat et al. 2005). We categorized bears as plateau or mountain based on the location of the hair snare or their capture location. Radiolocations from the live-captured bears indicated that they remained within the environment where they were captured (Ciarniello et al. 2002). We submitted all hair samples for DNA analysis (Wildlife Genetics International, Nelson, British Columbia, Canada) to identify individual bears and determine the species and sex of each bear and used only one hair sample from each individual bear. Paired guardhair and underfur samples from individual bears were obtained from the same barbed wire so that it was likely that these hair samples were derived from the same place on the body of one bear. Because all sampled guardhairs were collected prior to 2 July and were >9 cm in length, we assumed that the guardhair we sampled was fully grown and represented the annual assimilated diet from the previous year.

We washed hair samples in a 2:1 chloroform:methanol solution to remove surface oils, rinsed them with distilled water, and left them to air-dry for a period of 48 hours. For whole guardhair samples, we used between 1 and 3 entire guardhairs from each sample to meet the 0.8- to 1.2-mg weight guidelines for dual isotope analysis of animal tissue (University of California-Davis Stable Isotope Facility, Davis, California); 3–10 guardhairs were required for sectioned guardhair samples. Based on the number of hairs in an individual sample, we produced up to 3 replicates of guardhair, underfur, and guardhair sections. We cut samples and placed them in standard-weight 8 × 5-mm tin capsules (Elemental Microanalysis Limited, Okehampton, United Kingdom) and submitted them in microtiter plates for analysis (University of California-Davis Stable Isotope Facility). We analyzed 2 control samples after every 12 hair samples. To examine the magnitude of analytical variation relative to underfur and within-guardhair section variation for both $\delta^{15}N$ and $\delta^{13}C$, we tabulated the proportion of underfur and guardhair values that fell within 1 and 2 analytical standard deviations (SDs) of the individual section means.

Stable isotope ratios of carbon and nitrogen were measured by continuous flow isotope ratio mass spectrometry (20–20 mass spectrometer; PDZEuropa, Northwich, United Kingdom) after sample combustion to CO_2 and N_2 at 1,000°C in an on-line elemental analyzer (PDZEuropa ANCA-GSL). The gases were separated on a Carbosieve G column (Supelco, Bellefonte, Pennsylvania) before introduction to a Europa Hydra 20/20 isotope ratio mass spectrometer (D. Harris, University of California-Davis Stable Isotope Facility, personal communication). Results are expressed as a ratio in δ notation as parts per thousand (‰) using the equation of Peterson and Fry (1987).

We detected a correlation between $\delta^{15}N$ and $\delta^{13}C$ for guardhair ($P = 0.021$, $r = 0.17$, $n = 184$), and underfur ($P < 0.001$, $r = 0.54$, $n = 68$); however, we chose to examine each isotope separately because only a small amount of variation was accounted for. We randomly selected one guardhair and underfur sample from replicate samples for each individual bear. We subtracted the $\delta^{15}N$ and $\delta^{13}C$ underfur value from the paired guardhair value to obtain the difference in

isotopic values between guardhair and underfur for each paired sample. We first examined these differences for normality, then for homogeneity of variance using Bartlett's test, and then we compared them using a 2-way analysis of variance with population (i.e., mountain or plateau) and sex nested in population as the main effects. We conducted all statistical analyses using STATA (version 9; StataCorp 2005).

We assumed that guardhair was grown at a constant rate (Jacoby et al. 1999) and that hair began growing at different times throughout the spring and summer (C. T. Robbins, personal communication) but stopped growing when a bear entered into hibernation (S. D. Farley, Alaska Department of Fish and Game, personal communication). We cut hair into 30-mm sections and refer to the root section as S1 and sequential sections as S2, S3, S4, and S5. We discarded the distal end of guardhairs if the section was <30 mm long because the weight of this sample was generally <0.8 mg and, therefore, too light for isotopic analysis. Discarding this section precluded the comparison of sectioned hair with whole guardhair. Within each sample, we used guardhairs that were the same length, but hair length occasionally differed among replications for individual bears. We collected all hair samples in accordance with the Canadian Council of Animal Care guidelines, and techniques for bear captures were approved by the University of Alberta Animal Care Committee (Protocol 307204).

Results

The $\delta^{15}N$ and $\delta^{13}C$ values (Table 1) were within the range expected for grizzly bears that do not eat salmon. Within an individual, differences between guardhair and underfur $\delta^{15}N$ and $\delta^{13}C$ values varied significantly between mountain and plateau populations ($F_{1,56} = 6.90$, $P = 0.011$ for $\delta^{15}N$; $F_{1,56} = 4.88$, $P = 0.031$ for $\delta^{13}C$; Fig. 1). Within each population, however, there were no significant differences between guardhair and underfur for $\delta^{15}N$ and $\delta^{13}C$ between males and females ($F_{2,56} = 1.74$, $P = 0.18$ for $\delta^{15}N$; $F_{2,56} = 0.98$, $P = 0.38$ for $\delta^{13}C$). For $\delta^{15}N$, mean underfur values were higher than guardhair values but not significantly so for plateau males (i.e., in Fig. 1 the confidence interval [CI] includes 0). For $\delta^{13}C$, mean underfur values were lower than guardhair values, but significant only for mountain bears (Fig. 1).

For $\delta^{15}N$, the 95% CI around the root section of the guardhair (i.e., the portion of the hair most likely to have been grown at the same time as the underfur) overlapped the CI of the underfur for all but one bear (MM29; Fig. 2). For that mountain male bear (MM29) the $\delta^{15}N$ values for the underfur were different from all sections (Fig. 2). For most bears, however, the overlap between underfur and guardhair section $\delta^{15}N$ values was quite variable. Only for one mountain female (FM43; Fig. 2) did we observe a pattern of overlap that was consistent with the root section providing unique correspondence to the underfur $\delta^{15}N$ value. Similarly, for $\delta^{13}C$ the 95% CI around the root section of the guardhair overlapped the CI for the underfur for all but one bear (FM9; Fig. 3). Again, the overlap between the underfur and individual guardhair sections was quite variable.

The variation in $\delta^{15}N$ of underfur replicates was nearly consistent with the variation of the analysis ($SD_{analysis}$ for $\delta^{15}N = 0.12$, $n = 103$; samples from this study and unpublished data): 58% of the samples fell within 1 $SD_{analysis}$ of the replicate means and 92% fell within 2 $SD_{analysis}$ of the replicate means. On average, we would expect 68% and 95% of the observations to fall within 1 and 2 $SD_{analysis}$ (Sokal and Rohlf 1995), respectively, if all of the variation was from the analytical technique. In contrast, the $\delta^{15}N$ values for the individual guardhair replicates were much more variable: 47% fell within 1 $SD_{analysis}$ and 76% within 2 $SD_{analysis}$ of the replicate means. The variation in $\delta^{13}C$ for both underfur and guardhair section replicates could potentially be explained by just the analytical variation ($SD_{analysis}$ for $\delta^{13}C = 0.05$, $n = 103$; samples from this study and unpublished data). For underfur 79% and 92% of individual replicate values for $\delta^{13}C$ fell within 1 and 2 $SD_{analysis}$, respectively, of the individual replicate means. Unlike $\delta^{15}N$, the variation in $\delta^{13}C$ for guardhair sections was not much larger than the analytical error: 66% of the replicates fell within 1 $SD_{analysis}$ of their replicate $\delta^{13}C$ means and 85% fell within 2 $SD_{analysis}$.

Discussion

Differences in $\delta^{15}N$ and $\delta^{13}C$ values between guardhair (annual assimilated diet) and underfur (autumn assimilated diet) indicated that autumn assimilated diet differed from the average annual assimilated diet for both populations that we examined (Fig. 1). Given that the isotopic values of $\delta^{15}N$ and $\delta^{13}C$ are higher in meat sources than plant sources (see Hilderbrand et al. 1996, Jacoby et al. 1999, Hobson et al. 2000, Felicetti et al. 2003, Ben-David et al. 2004 for representative isotopic values of grizzly bear foods), we would expect that both $\delta^{15}N$ and $\delta^{13}C$ values would be higher in underfur if grizzly bears ate more meat in the autumn and lower if grizzly bears ate more plants in the autumn. Our data did not conform to either expectation because $\delta^{15}N$ values for underfur were higher than $\delta^{15}N$ values for guardhair, whereas $\delta^{13}C$ values for underfur were lower than $\delta^{13}C$ values for guardhair (Fig. 1).

Higher $\delta^{15}N$ values in underfur, suggesting more meat in the autumn diet, are consistent with the seasonal feeding habits of grizzly bears observed in our study area (Ciarniello et al. 2002) and elsewhere (Servheen 1983, Mattson et al. 1991, McLellan and Hovey 1995), where meat or ant consumption by grizzly bears is higher in autumn. In contrast with $\delta^{15}N$, $\delta^{13}C$ values were lower in underfur, suggesting that bears ate less meat in the autumn than throughout the year. However, the difference in $\delta^{13}C$ values between guardhair and underfur $\delta^{13}C$ values was slight, and those $\delta^{13}C$ values were within the range of variation for mammals on a constant diet (see Hobson et al. 1996). An increase in $\delta^{13}C$ values resulting from higher meat consumption in autumn may be offset by lower $\delta^{13}C$ values

Table 1. Mean and variation of $\delta^{15}N$ and $\delta^{13}C$ values for whole guardhair and underfur for grizzly bears by sex and population for grizzly bear hair samples collected from 1998 to 2002 in central British Columbia, Canada.

			$\delta^{15}N$ (‰)				$\delta^{13}C$ (‰)			
			Guardhair		Underfur		Guardhair		Underfur	
Population	Sex	*n*	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Mountain	M	11	2.83	1.15	4.11	0.86	−23.20	0.39	−23.60	0.34
	F	30	2.80	1.03	3.59	0.95	−23.14	0.36	−23.36	0.44
Plateau	M	9	5.10	1.01	5.54	1.18	−23.05	0.63	−23.14	0.89
	F	10	5.12	1.44	5.63	1.36	−23.16	0.92	−23.24	1.01

in autumn plant foods. Berries, for example, have a substantially lower $\delta^{13}C$ value than forbs (Ben-David et al. 1997, Hobson et al. 2000) and grizzly bears, both in our study area (Ciarniello et al. 2002) and elsewhere (Servheen 1983, Mattson et al. 1991, McLellan and Hovey 1995), feed more on forbs in spring and on berries in autumn.

Differences in isotopic values for hairs grown during different periods may not be entirely due to differences in assimilated diet but also could be attributed to seasonal differences in metabolism. The stable isotope approach to diet interpretation is possible because consumer tissues reflect the stable isotope values in their diet (Hobson et al. 2000). Organisms preferentially assimilate the heavier isotope and excrete the lighter one (Hilderbrand et al. 1996), but the metabolic processes involved may vary among diet types, season, and other factors (Hobson et al. 2000, Keeling and Nelson 2001, Felicetti et al. 2003). Proportions of meat in the assimilated diet may be misrepresented, depending on whether bears are using food resources for energy or fat accumulation (Hobson et al. 2000). Food acquired by grizzly bears in the spring is mostly directed toward lean body mass (Hilderbrand et al. 1999*a*) and in the autumn is primarily stored as fat (Barboza et al. 1997, Hilderbrand et al. 1999*a*). Felicetti et al. (2003) warned against using carbon isotopes to estimate assimilated diets because their feeding trial data showed that carbon isotope signatures in grizzly bear plasma did not track dietary carbon

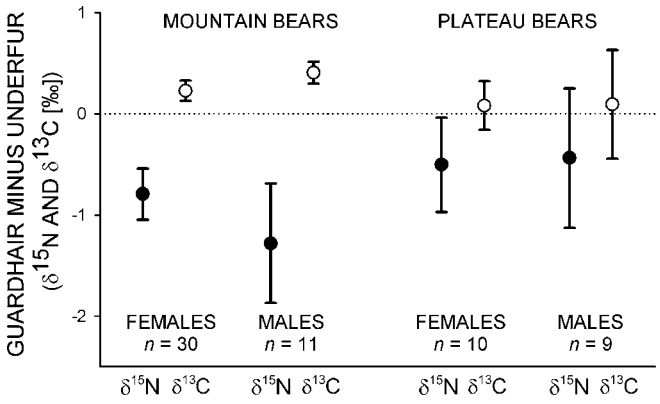

Figure 1. Mean and 95% CIs for paired guardhair minus underfur values of $\delta^{15}N$ and $\delta^{13}C$. Confidence intervals that encompass zero indicate that there is no difference between mean guardhair and underfur values for that category for grizzly bear hair samples collected from 1998 to 2002 in central British Columbia, Canada.

signals as well as nitrogen tracked its dietary signal. In the absence of information on the influence of metabolic processes on isotopic values, and baseline data on isotopic variation within a hair tissue for grizzly bears on a constant diet, we cannot determine whether the differences we observed between guardhair and underfur are the result of dietary or metabolic influences on isotopic values. The differences we observed between $\delta^{15}N$ values for guardhair and underfur, however, were beyond the range observed for seals on a constant diet (Hobson et al. 1996), suggesting that differences may be partially attributed to differences in diet. Studies that quantify isotopic variation within hair tissue for bears on a constant diet across different seasons are needed to resolve this issue.

If the assimilated diet of the bears for which we sectioned guardhairs is the same as for those bears in Fig. 1, and our assumptions that underfur is grown only in the autumn and that guardhair grows throughout the entire year including the autumn are correct, then we would expect 1) variation among guardhair sections for individual bears, and 2) underfur isotope values to be most similar to the guardhair section nearest the root. When we examined sectioned guardhair values for individual bears (Figs. 2 and 3), primarily mountain females, we found that patterns along guardhairs for individual bears varied considerably and that high CIs were associated with samples having only 2 replicates (i.e., FM11, FP34, and MM45). Despite variation within replicates, however, differences among sections were still apparent for some bears (e.g., FM43). Isotopic values ($\delta^{15}N$ and $\delta^{13}C$) for the section of guardhair nearest the root overlapped with the underfur isotopic values for 7 of 8 bears. Overlap with subsequent sections was highly variable. Our sectioning approach and sample sizes, however, precluded our testing for differences among sectional means within individual bears. Quantifying the variation in isotopic values among individual guardhair sections will be possible only when analytical techniques are sensitive enough to measure individual hair segments.

If all guardhair grows at a constant rate and stops growing at the same time in the autumn, then variation in isotope values within guardhair sections of a fixed length should vary within analytical error ($SD_{analytical}$). For underfur, variation in $\delta^{15}N$ and $\delta^{13}C$ did fall within the expected bounds of analytical error. Although variation in $\delta^{13}C$ among sections for individual bears was close to the expected analytical error, this was not the case with the $\delta^{15}N$ values.

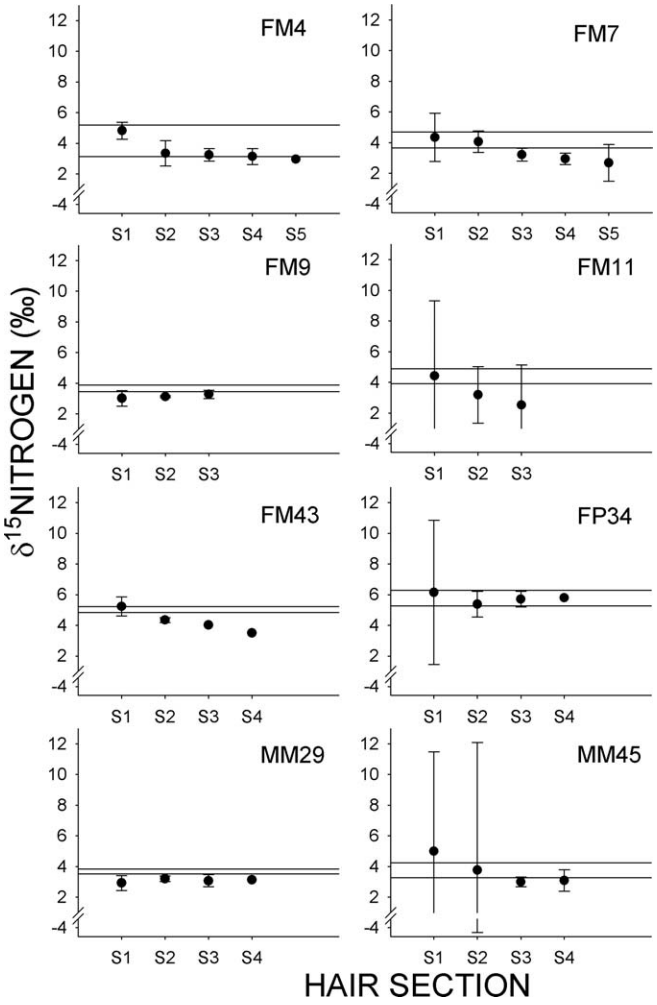

Figure 2. Mean and 95% CIs for $\delta^{15}N$ values of guardhair sections (dots and vertical bars) for individual grizzly bears (M = mountain, P = plateau; M = male, F = female) compared with 95% CIs of underfur (horizontal lines) for grizzly bear hair samples collected from 1998 to 2002 in central British Columbia, Canada. We cut hair into 30-mm sections and refer to the root section as S1 and to sequential sections as S2, S3, S4, and S5.

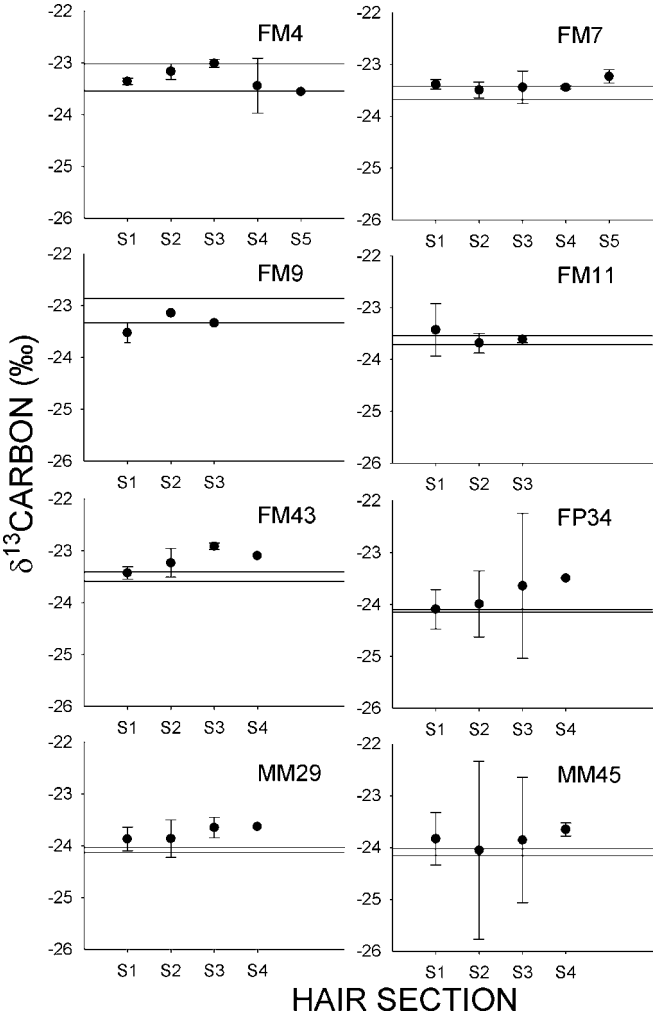

Figure 3. Mean and 95% CIs for $\delta^{13}C$ values of guardhair sections (dots and vertical bars) for individual grizzly bears (M = mountain, P = plateau; M = male, F = female) compared with 95% CIs of underfur (horizontal lines) for grizzly bear hair samples collected from 1998 to 2002 in central British Columbia, Canada. We cut hair into 30-mm sections and refer to the root section as S1 and to sequential sections as S2, S3, S4, and S5.

Because variation in $\delta^{15}N$ within sections exceeded variation explained by analytical error, we concluded that one or both of our assumptions about hair growth may be incorrect. Therefore, researchers should be cautious about making diet inferences using sectioned guardhairs because assumptions about hair growth likely are not met and, at present, cannot be adequately tested.

Management Implications

Studies examining diets of different populations should consider utilizing underfur to represent autumn assimilated diet, because we found a significant difference in isotopic values between whole guardhair and underfur. We recommend that using both guardhair as a representation of annual assimilated diet and underfur as a representation of autumn assimilated diet will provide better insight into differences in diet among bear populations. Differences in $\delta^{15}N$ and $\delta^{13}C$ values among underfur and sections of guardhair suggest that sectioning guardhair has the potential to resolve diet at a finer-than-annual diet scale, if assumptions about hair growth have been met. Assumptions about the rate, onset, and cessation of hair growth must be considered in the context of specific research objectives. Understanding the temporal pattern of hair growth and quantifying isotopic variation along the hair length for grizzly bears on a constant diet would greatly contribute to interpretation of isotopes in hair sections.

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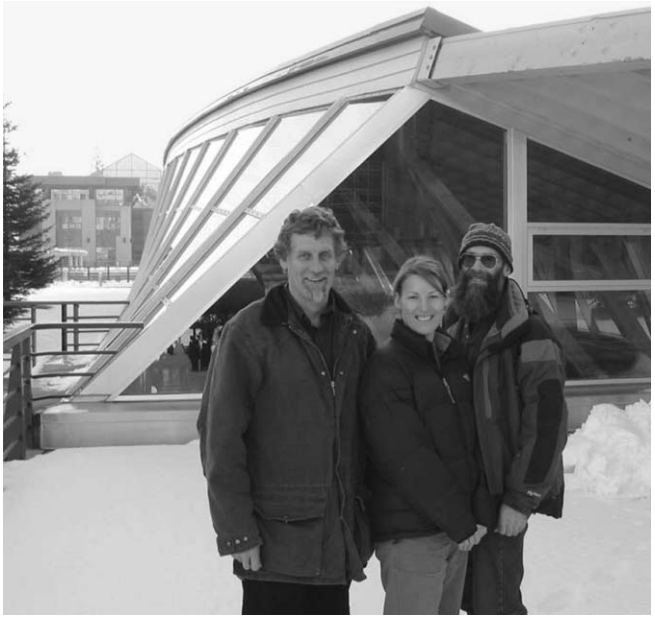

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