

DIET AND MORPHOLOGY OF EXTANT AND RECENTLY EXTINCT NORTHERN BEARS

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Abstract: I examined the relationship of diets to skull morphology of extant northern bears and used this information to speculate on diets of the recently extinct cave (*Ursus spelaeus*) and short-faced (*Arctodus simus*) bears. Analyses relied upon published skull measurements and food habits of Asiatic (*U. thibetanus*) and American (*U. americanus*) black bears, polar bears (*U. maritimus*), various subspecies of brown bears (*U. arctos*), and the giant panda (*Ailuropoda melanoleuca*). Principal components analysis showed major trends in skull morphology related to size, crushing force, and snout shape. Giant pandas, short-faced bears, cave bears, and polar bears exhibited extreme features along these gradients. Diets of brown bears in colder, often non-forested environments were distinguished by large volumes of roots, foliage, and vertebrates, while diets of the 2 black bear species and brown bears occupying broadleaf forests contained greater volumes of mast and invertebrates and overlapped considerably. Fractions of fibrous foods in feces (foliage and roots) were strongly related to skull morphology ($R^2 = 0.97$). Based on this relationship, feces of cave and short-faced bears were predicted to consist almost wholly of foliage, roots, or both. I hypothesized that cave bears specialized in root grubbing. In contrast, based upon body proportions and features of the ursid digestive tract, I hypothesized that skull features associated with crushing force facilitated a carnivorous rather than herbivorous diet for short-faced bears.

Ursus 10:479–496

Key words: *Ailuropoda melanoleuca*, *Arctodus simus*, black bear, brown bear, cave bear, food habits, giant panda, polar bear, short-faced bear, skull morphology, *Ursus americanus*, *Ursus arctos*, *Ursus maritimus*, *Ursus spelaeus*.

An animal's diet can reveal much about its relationship to the physical environment and other organisms in it. For example, Ewer (1973), Eisenberg (1981), and several authors in Gittleman (1989) describe pervasive associations among the physiology, morphology, behavior, and diet of numerous taxa, including carnivores. This type of research strongly suggests that diet should closely reflect the constraints and adaptations of somatic features while influencing the evolutionary trajectory of these same traits. At the very least, we would expect correlation, subject to judicious interpretation of functional relationships (Radinsky 1985).

The common associations between physical form and diet of extant organisms have led researchers to speculate on the diets and other life habits of extinct species based on shared skeletal traits, especially of the skull and limbs (e.g., Kurtén 1967, 1976; Radinsky 1981a; Van Valkenburgh 1985, 1988, 1989). Given that fossilized or otherwise preserved body parts are the only tangible clues left to inform us about the behavior of vanished species, establishing relationships between, for example, diet and skull morphology of extant organisms is our only means of imbuing these physical remains with useful information (Radinsky 1985, Guthrie 1990). Knowledge about the behavior of recently extinct forms can, in turn, help us better understand why surviving species that existed with these vanished animals behave the way that they do.

Although recent work (e.g., Davis 1949, 1964; Radinsky 1981a; Gittleman and Harvey 1982; Van Valkenburgh 1985, 1988, 1989; Gittleman 1986a,b;

McNab 1986) has placed the diet, behavior, and skeletal morphology of bears in context of other carnivores, little has been done to examine relationships among ursids between their physical form and foods. There are some descriptive (e.g. Bromlei 1965, Schaller et al. 1989) and analytical comparisons (Davis 1964, Stirling and Derocher 1990), but there are no quantitative analyses of relationships between morphological and dietary patterns. Regardless, the diverse ursid skull morphology (Radinsky 1981a) holds promise of being related to either mechanical or evolutionary forces associated with diet.

I used quantitative and other analytical techniques to explore relationships between diets and morphology of extant bear species and used this information to speculate on the diets and related behavior of other bears that went extinct within the last 15,000 years. My analysis uses existing published information and is intended to serve several purposes: elucidate meta-patterns, precipitate more informed hypotheses, and stimulate further research. I also undertook this analysis with relatively little concern for whether the apparent relationships between diet and physical form were genetically fixed or merely the result of mechanical forces during development. In either case, the analysis would have bearing on both short- and long-term morphological adaptations as well as diets of extinct bears.

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METHODS

Data and Data Structuring

The paucity of information on bears from tropical and subtropical latitudes (i.e., the sun [*Helarctos malayanus*], sloth [*Melursus ursinus*], and Andean [*Tremarctos ornatus*] bears) led me to focus on extant and recently extinct bears of temperate, boreal, and arctic regions. These constitute a logical assemblage of species that have to some extent co-existed, if not co-evolved. Of surviving bears, I examined the polar, brown, American black, and Asiatic black bears and the giant panda. Of recently extinct bears, I examined the cave and giant short-faced bears. The skeletal morphology of cave and short-faced bears has been examined in relative detail by Kurtén (1955, 1958, 1967, 1976); more recently the short-faced bear was studied by Emslie and Czaplewski (1985). I followed the classification and nomenclature of Wozencraft (1989) and the corroborating evidence of Goldman et al. (1989) in treating the giant panda as a bear. The panda and polar bear defined dietary and morphological end-points for the analysis.

Data published by other authors were used for all analyses. Common skull measurements were available for individual bears from different studies and areas (sources listed in App. 1). These measures are defined in Figure 1, along with a measure of snout or rostrum length (the rostral end of the orbit to the rostral end of the skull—FL) that I derived from published photographs. I used a dental index (DENTA) that was the summed products of mean length and width for the P⁴, M¹, and M² teeth (total length of this dental row [DENTL] is illustrated in Fig. 1). All these measures, to some extent, have been associated with either diet or forces relevant to explaining diet in other taxa especially of primates and ungulates (e.g., Moss 1968, Kay 1975, Corruccini 1980, Preuschoft et al. 1986, Janis and Ehrhardt 1988, Spencer 1995).

I averaged all measures, by taxon, based on individual study means, for use in the exploratory analyses because not all skull measures were available from each source, sample sizes differed dramatically for each measure and species, and some results were presented as means and others by individual skull. As a consequence, multivariate analyses were strongly oriented to the equivalent of taxa centroids. Except for brown bears these taxa corre-

sponded to species. Brown bear subgroups were distinguished on the basis of subspecies from Pacific coastal, European, and interior continental (North America and Asia) regions. This stratification was consistent with major morphological dissimilarities among subspecies identified by Ognev (1931) and Hall (1984).

I also included measures of body size and relative skeletal dimensions for comparison among species. Skeletal dimensions were expressed as previously defined indices: FMT = femur length/longest metatarsal length (Van Valkenburgh 1985); VHR = humerus + radius length/length of thoracic vertebrae 10, 11, and 12 (Davis 1964); RH = (radius/humerus length) × 100 (Davis 1964, Emslie and Czaplewski 1985); and HW = (humeral width across epicondyles/humeral length) × 100 (Hildebrand 1985). Increasing values of HW and decreasing values of RH reflected potential adaptations to digging, while increasing VHR and decreasing FMT values reflected potential adaptations to increased terrestrial mobility.

Information from 85 studies of bear diet representing all 6 extant species were used for this analysis (see App. 2 for references). Other studies reported food habits or described feeding behavior, but in ways that I could not use. Most studies used in this analysis pertained either to Eurasian brown bears ($n = 21$), North American grizzlies ($n = 22$) or American black bears ($n = 32$). Diet was represented as fecal content for the period corresponding to late summer and fall hyperphagia. I assumed that the bulk of high quality food was consumed annually during this period (Nelson et al. 1983, Mattson et al. 1991). Nelson et al. (1983) further argued that hyperphagia is the time of year most critical to survival and reproduction of black and brown bears. The diet during hyperphagia thus has the greatest potential relevance to explaining morphological patterns. This period likely varies with habitat conditions, so I judged the onset and end of hyperphagia by descriptions, if available, of bear behavior for each area and the advent of high quality mast in the diet. By this approach, with the exception of polar bears and pandas, hyperphagia began in July and ended in October or November.

Scat contents (either by percent volume or some index of percent volume) were averaged for the season, weighted by sample sizes, and averaged across years. Each year was weighted equally unless annual sample sizes were extremely disparate. A few ($n = 14$) key studies only provided frequency of diet item occurrence. These were used (standardized so as to sum to 100%), realizing that, in contrast to volumes, frequencies may inflate contributions, especially of invertebrates (i.e., where both frequency and volume had been recorded,

invertebrates were consistently a frequent but low volume part of scats).

Diets were described in terms of 6 broad categories: foliage, roots, soft mast, hard mast, invertebrates, and vertebrates. These categories reflected either markedly different nutrient composition, physical structures, or bear foraging behavior, with potential relevance to differences in bear morphology. Hard mast consisted of fruits and seeds with a hard protective covering (including both acorns and pine [*Pinus* spp.] seeds), while soft mast consisted of fleshy fruits or even strobili (such as those of *Juniperus*) that were comparably soft. These categories thus did not have clear anatomical or taxonomic distinction, but rather related to features of greater potential relevance to how bears used them. For some analyses, these 2 categories were pooled simply as "mast." Foliage and roots were similarly pooled as fibrous foods, recognizing that they shared the com-

mon trait of potentially high fiber content, although one was procured by grazing or browsing and the other by the considerably more demanding process of grubbing. Invertebrates were distinguished by their small size and typical chitinous exoskeleton, while vertebrates included tissue acquired by diverse behavior including grubbing, scavenging, and both terrestrial and aquatic predation.

The primary stratification I used for analysis of dietary differences reflected both bear taxonomy and structure of the study area vegetation. Food habits studies were segregated on the basis of the investigated species and, for brown and American black bears, by whether the predominant study area vegetation was non-forest (i.e., arctic or alpine), or coniferous, mixed, or pure broadleaf forest. Determination of vegetation structure was based on study area descriptions and the ecoregion (Bailey 1989) within which the study area was located. I hypothesized that the availability and use of different bear foods was

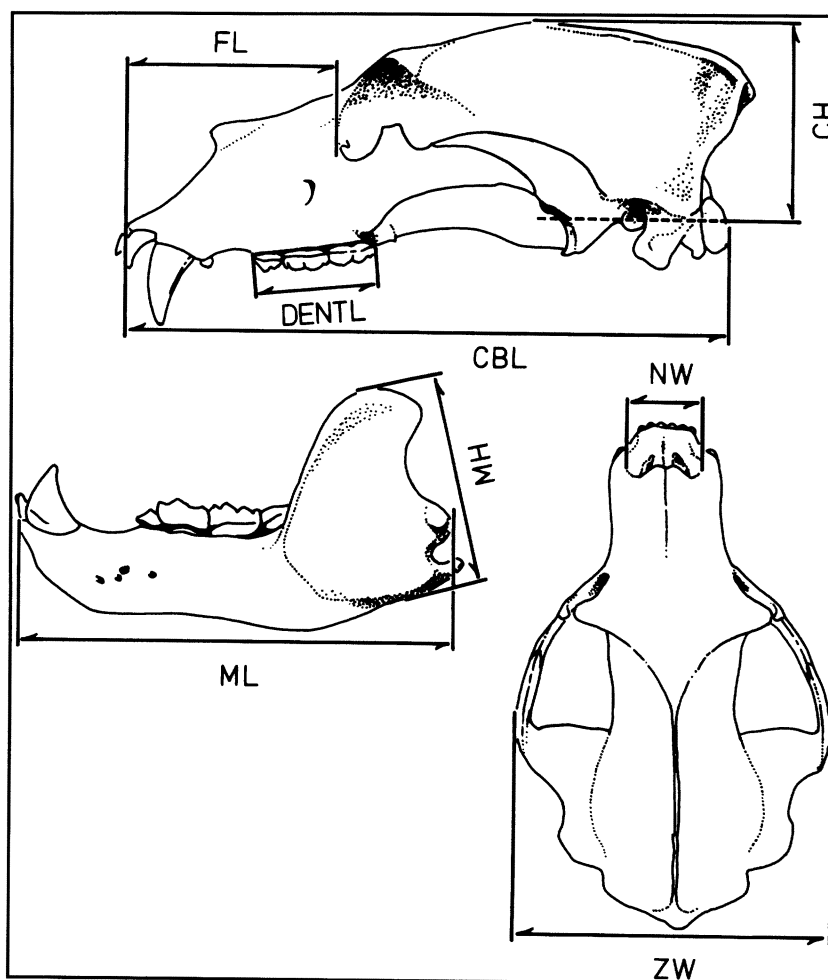


Fig. 1. Measurements used in principal components (PC) analysis of ursid skulls.

fundamentally related to these broad differences in vegetation structure (e.g., hard mast would be more abundant in broadleaf forests, soft mast relatively more abundant in coniferous forests, and roots and vertebrates relatively more abundant in nonforest areas). Finally, to match the analysis of skull shape, I stratified food habits studies by species, and for brown bears, additionally by those subspecies along the Pacific rim, in interior regions of Asia and North America, and in Europe.

The stratifications that I used for this analysis mixed intra- and interspecific variation. Subspecies and groupings based upon vegetation structure were recognized in addition to species. This approach was consistent with my premises: that physical form, whether genetically fixed or mechanically reinforced, was both a reflection and determinant of diet; further, prevailing vegetation structure was a factor, in addition to bear morphology, that influenced diet. In any case, taxonomy represents relatively artificial distinctions, highlighted by the likelihood that polar bears are genetically no more distinct from brown bears than brown bears are genetically diverse among themselves (Cronin et al. 1991).

Analysis

I used principal components (PC) analysis to reduce the numerous and somewhat arbitrary measures of skull and dental morphology (including both extant and extinct species) to fewer dimensions that were theoretically related to more fundamental features of skull morphology (Wilson 1976, Radinsky 1981*b*). Rather than control for allometric effects prior to PC analysis by, for example, using standardized residuals from relationships with skull length or body mass (Radinsky 1981*b*), I simply used natural-log transformations of the raw values. The first PC thus described substantial size-related correlations of skull measurements (i.e., allometric effects), while subsidiary PCs were of primary interest because they described variation in skull morphology independent of size. Loadings of skull variables on PCs were used for functional interpretations, while species scores were used to describe relationships between skull morphology and mean diet as well as morphological relationships among species.

I used multiple analysis of variance and canonical discriminant analysis to test for and describe differences in diet among bear species, subspecies, and bear populations grouped by dominant vegetation structure. If diets differed for all bear types (at $\alpha = 0.1$), I used a multivariate analog of the protected least significant difference procedure based upon pair-wise Hotellings' T^2 to identify individual types that were not different (Johnson and

Wichern 1992). I used these tests, coupled with Mahalanobis distances, to characterize pair-wise dissimilarities between diets of different bear types. I interpreted dietary differences between types by examining the canonical coefficients of dietary categories for each canonical variable, conditioning my interpretation upon their eigenvalues and the proportion of variation that they explained. I used ranked values in these multivariate procedures as a nonparametric approach that reconciled parametric techniques with non-normal data (i.e., proportions) (Conover and Iman 1980, 1981). I also weighted each study in these analyses by the number of years and feces that had been sampled ($100 \times \{(\text{number of years} + \text{number of feces})/2\}$, where years and feces were scaled to be ≤ 1 , which corresponded to the maximum value observed for each in any study). I deleted 1 dietary category (invertebrates) from these analyses to alleviate the linear non-independence that would have otherwise arisen from the proportions summing to 1. In addition to these multivariate procedures, I also report univariate tests (analysis-of-variance [ANOVA] and multiple comparisons) for differences among means for each dietary category, again using ranked data.

Because I wanted to predict diets of 2 extinct bear species, I related skull morphology to diet through least-squares multiple linear regression analysis, with diet item fraction dependent on skull morphology of extant bears. I used logits of mean fractions for each diet item (see Aitchison's [1986] use of log-ratio transformations in the analysis of compositional data) and species scores from the first 3 PCs for the 7 groupings of extant bear species (pandas, polar bears, the 2 black bear species, and 3 groupings of brown bear subspecies). Although, *a priori*, the dependence of diet upon skull morphology is equivocal and independent variables were measured with error, this predictive approach is compatible with exploratory analysis and hypothesis generation (Gilbert 1989:33). I did not use canonical correlation analysis because of prohibitively small sample sizes and my interest in elucidating relationships between skull morphology and bear use of specific diet items. The relationship of fibrous foods in the diet to skull morphology was so strong (see below) that this result would have been prominent, regardless of which statistical method I used.

RESULTS

Diets

The diets of extant bears are diverse (Table 1). Giant pandas and polar bears were distinguished, *a priori*, by

near exclusive folivory and carnivory, respectively. Diets of the remaining 3 species were also different, globally (Wilks' $\Lambda = 0.545$; 10, 148 df; $P < 0.001$) and from each other. Considering groupings that also reflected the dominant vegetation structure of each study area, there was an aggregate difference in diets (Wilks' $\Lambda = 0.199$; 25, 265 df; $P < 0.001$) and pairwise differences among most groupings (Table 2). Only 2 pairwise contrasts were not significant. Diets of American black bears that occupied broadleaf forests did not differ from diets of Asiatic black bears (also almost exclusively residents of broadleaf forests), and diets of brown bears that occupied arctic or alpine areas did not differ from diets of brown bears that occupied coniferous forests. Otherwise, among the bears with more diverse diets, Asiatic black bears and brown bears living in arctic or alpine regions exhibited dietary extremes characterized by large volumes of hard mast and by large volumes of vertebrates and roots, respectively (Tables 1 and 2).

The first 3 canonical variables generated by canonical discriminant analysis were significant and collectively described 96% of the variation in diets among the groupings based on bear species and vegetation structure (Table 3). The first canonical variable primarily described a gradient from diets rich in roots, vertebrates, and foliage to one rich in mast, or basically a gradient from foods typical of brown bears in colder climates and more open habitats to foods typical of black bears in warmer forests (Fig. 2). The second and third canonical variables described gradients related more to trade-offs between soft mast, and hard mast and roots (the latter typified by the diet of grizzly bears in the interior contiguous United States [Mattson et al. 1991, Craighead et al. 1982]), and between vertebrates and roots and soft mast (the latter typified by the diet of grizzly bears in much of interior Canada and Alaska), respectively.

Among the species with more diverse diets, black bears were typified by the consumption of mast, with hard mast a more common food for black bears occupying broadleaf forests (Table 1, Fig. 2). Black bears living in coniferous forests consumed proportionately more soft mast than bear species living anywhere else. With the exception of populations living in broadleaf forests, brown bears were distinguished by consuming greater relative volumes of vertebrates and roots. Interestingly, the diet of brown bears living in broadleaf forests substantially overlapped the diet of black bears, suggesting that vegetation structure, as much as species, was a controlling factor.

Not considering the self-evident differences in diets of giant pandas and polar bears, the diets of other taxa

used for relating diet to skull morphology (i.e., American and Asiatic black bears, and Pacific coastal, European, and interior continental subspecies of brown bear) were also statistically distinct (Wilks' $\Lambda = 0.160$; 20, 223 df; $P < 0.001$). Aggregate diets differed primarily by root, soft mast, vertebrate, and hard mast volumes (in order of loading on canonical variables). All taxa differed by pair-wise comparisons, except the diet of coastal brown bears did not differ from the diet of continental brown bears. By individual diet category (Table 2), American black bears ate more soft mast than did continental brown or Asiatic black bears, while Asiatic black bears ate more hard mast and continental brown bears ate more roots than any other type except coastal brown bears.

Skulls

Principal components analysis effectively reduced the 9 measured skull dimensions to 3, accounting for 99% of total variation (Table 4). Similar positive loadings for all skull dimensions on PC1 reflected substantial size-related correlation among these measures (i.e., allometric relationships). Although there was relatively little variation residual to PC1, this residual variation was nonetheless of great interest because it characterized skull *shape* and presumed associations with diet (e.g., adaptations), aside from *size per se*. Dental surface area, cranial and mandibular height, and zygomatic width exhibited positive loadings on PC2. These measures have either been positively associated with muscle size (primarily of the temporal and masseter) or with increased dental surface area that together provide for greater crushing capability (Davis 1964, Kay 1975, Greaves 1978, Radinsky 1981*b*, Demes et al. 1986). The negative loading of nasal width (NW) and the positive loadings of "face" and mandible lengths (FL and ML) on PC3 indicate a comparatively narrow and elongate snout at high values and a broad and short snout at low values.

The main *Ursus* lineage was clustered in PC2 x PC3 space separate from the giant panda and short-faced bear (Fig. 3). As expected (Davis 1964), the giant panda exhibited the greatest presumed adaptations for exerting crushing force at the occlusal plane. Also as expected (Kurtén 1967), the short-faced bear was distinguished by the shortest and broadest snout of all taxa, together with moderate apparent crushing capabilities. Taxa within the genus *Ursus* varied from the polar and American black bears, with relatively little crushing capability and shorter, broader snouts, to the cave bear, which combined a relatively long snout with relatively greater apparent adaptations to crushing. The black bears exhibited

Table 1. Mean percent volume of diet items in feces of northern bears, averaged over individual studies. Means not different at $\alpha = 0.1$ (based on ranks) are followed by the same letters in columns, only including taxa with sample sizes $n > 5$. Brown bears and American black bears are geographically stratified in 2 ways that are described in the text, with statistical groupings for the 2 classifications separated by a '/'. Values do not sum exactly to 1 across rows because values for each type of diet item are averaged over individual studies.

Taxa/Geographic groupings	No. studies (<i>n</i>)	Feces composition (% volume)					
		Foliage	Roots	Soft mast	Hard mast	Invertebrates	Vertebrates
Giant panda	2	99.0	0.0	0.1	0.0	0.0	0.1
Polar bear	2	1.0	0.0	1.0	0.0	0.0	97.5
Asiatic black bear	7	15.2b/b	0.0b/b	34.8b/b	43.1a/a	5.4abcd/bc	2.4b/b
American black bear (1)							
Broadleaf forest	16	22.8b/	1.4b/	49.4ab/	20.0a/	5.9abc/	4.1ab/
Coniferous forest	16	23.6ab/	0.0b/	61.2a/	1.4b/	4.4abc/	3.5b/
American black bear (2)	32	19.5 /ab	0.1 /b	55.3 /a	10.7 /b	5.1 /ab	3.8 /bc
Brown bear (1)							
Broadleaf forest	15	22.8ab/	1.4b/	46.9b/	7.8b/	12.2a/	9.0ab
Coniferous forest	19	30.9a/	9.2a/	39.5b/	7.0b/	3.0bcd/	7.5ab
Arctic/alpine	9	26.2ab/	14.0a/	38.5c/	0.0b/	0.8cd/	20.6a
Brown bear (2)							
European	12	20.7 /ab	0.2 /b	48.4 /ab	2.5 /b	14.5 /a	13.3 /a
Continental	23	29.9 /a	12.4 /a	37.1 /b	5.6 /b	2.0 /c	10.9 /ab
Pacific coastal	8	28.4 /ab	4.3 /ab	45.5 /ab	11.4 /ab	3.5 /abc	6.9 /ab

a modal, conceivably more generalized skull shape. The closely related polar, brown, and cave bears (Kurtén 1964, 1976; Shields and Kocher 1991) all displayed a substantial diastema separating the canines from premolars, although this gap was most pronounced in the cave bear (Fig. 3b).

Relationships of Diet to Skull Morphology

There was a strong linear relationship between fibrous foods (\hat{Y}) and PC1 and PC2 ($R^2 = 0.97$; 2,4 df; $F = 76.0$; $P < 0.001$):

$$\hat{Y} = -0.122 + 0.331PC1 + 3.38PC2$$

Fibrous foods were comprised of foliage and roots added together (\hat{Y} , as a logit, where diet fraction [p] = $e^{\hat{Y}-0.01}/[1+e^{\hat{Y}-0.01}]$). Standardized coeffi-

cients for PC1 and PC2 were 0.272 and 1.004, respectively; both coefficients were also significantly different from zero. In other words, relative volumes of fibrous foods in the feces of extant bears were related, first, to apparent adaptations of the skull to crushing and, second, to larger size. A naive extrapolation from this relationship would predict that cave bear feces, on average, contained 84% fibrous foods and that short-faced bear feces contained 87% fibrous foods during hyperphagia (Fig. 4). No other diet category exhibited a statistically significant relationship to PCs describing skull morphology.

Other Morphological Considerations

The short-faced bear skull exhibited some additional interesting and potentially diagnostic features. Its snout

Table 2. Pair-wise Mahalanobis distances (D^2) between northern bears based on ranked dietary composition of feces, not considering invertebrates. The giant panda and polar bear were excluded because of small sample sizes. Pairwise comparisons denoted by an * were significantly different ($\alpha = 0.1$, using Hotellings' T^2).

Taxa/Geographic groupings	Taxa/Geographic groupings				
	Asiatic black bear	American black bear—broadleaf forest	American black bear—coniferous forest	Brown bear—broadleaf forest	Brown bear—coniferous forest
American black bear—broadleaf forest	0.12				
American black bear—coniferous forest	0.54*	0.34*			
Brown bear—broadleaf forest	0.35*	0.19*	0.13*		
Brown bear—coniferous forest	0.91*	0.67*	0.54*	0.42*	
Brown bear—arctic or alpine	1.14*	0.79*	0.42*	0.53*	0.16

Table 3. Standardized canonical coefficients for diet variables and means for groupings of northern bears on the first 3 canonical variables from canonical discriminant analysis ($n = 82$). Eigenvalues, proportion of total variation, and significance are also given for each canonical variable. Invertebrates were excluded from the analysis to achieve linear independence, and polar bears and giant pandas were excluded because of small sample sizes.

	Canonical variable		
	CAN1	CAN2	CAN3
Diet variables			
Foliage	0.328	-0.317	-0.142
Roots	1.299	0.533	0.364
Soft mast	0.183	-0.448	0.359
Hard mast	-0.337	0.675	-0.144
Vertebrates	0.391	-0.130	-0.919
Bear groupings			
Asiatic black bear	-0.504	0.251	0.031
American black bear—broadleaf forest	-0.386	0.145	0.107
American black bear—coniferous forest	-0.125	-0.350	0.042
Brown bear—broadleaf forest	-0.170	-0.100	-0.182
Brown bear—coniferous forest	0.415	0.141	-0.052
Brown bear—arctic/alpine	0.441	-0.145	0.214
Eigenvalue	1.325	0.466	0.197
Proportion of variation	0.683	0.196	0.083
Significance	<0.001	<0.001	0.018

is relatively the widest and flattest of the examined bear species, visually most similar to that of the polar bear and markedly dissimilar to the black and brown bears (Fig. 5). Among extant bears (based primarily upon interpretations of the polar bear skull) and other carnivores, this feature is thought to facilitate delivery of a killing bite to prey and consumption and dismemberment of larger carcasses (Kurtén 1964, Ewer 1973, Radinsky 1981b). The short-faced bear's skull is also remarkably similar in both profile and top view to that of the spotted hyena (*Crocuta crocuta*) (Fig. 6), except that its teeth are proportionally smaller and the cusps less developed.

Body sizes and skeletal proportions also offered insight into possible diets of the 2 extinct bear species (Table 5). The giant short-faced bear had relatively the longest metatarsals (low FMT) and forelegs (high VHR) of any bear, with the latter measure in range of other carnivores that were pursuit rather than ambush hunters. By contrast, the cave bear had short metatarsals and legs compared to all other bears except the panda and polar bear. However, compared to other carnivores, all bears had short metatarsals (Table 5). Relative to known specialized scratch diggers (Hildebrand 1985), the short-faced bear had slender and the cave bear comparably robust humeri, with a trend towards similarly short radii (low RH) in the cave bear. Naively assuming that the short-

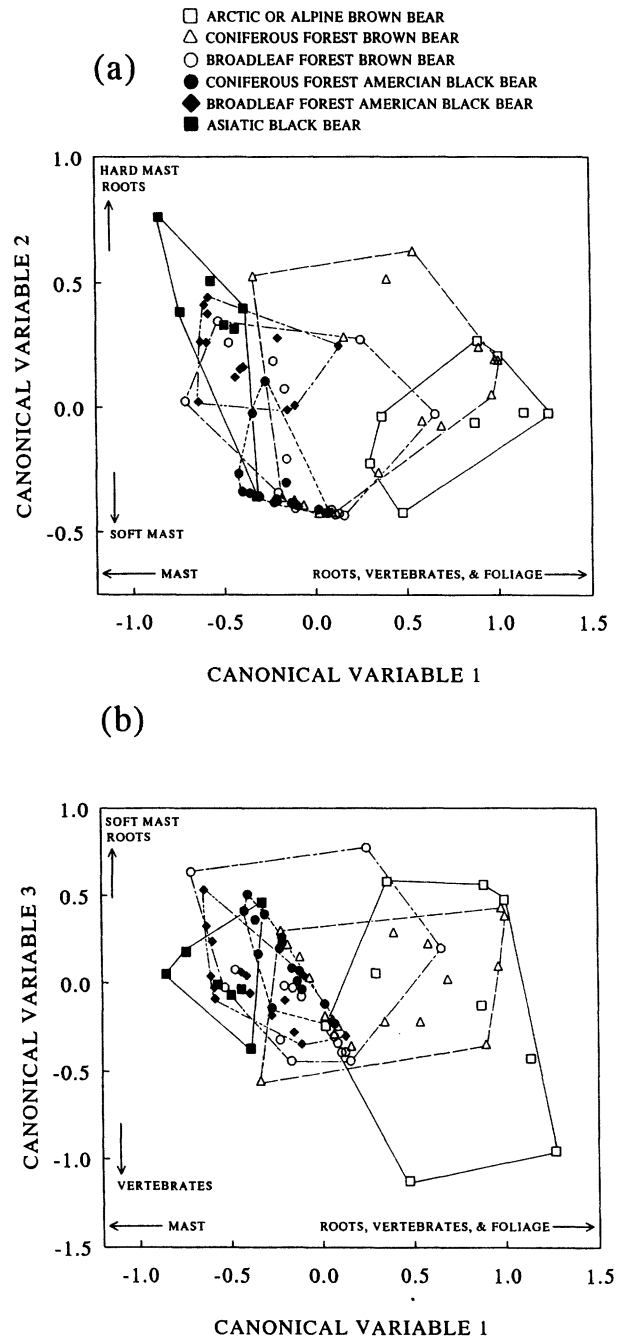


Fig. 2. Groupings of extant northern bear are plotted with respect to the (a) first and second and (b) second and third canonical variables (CANs), from canonical discriminant analysis of fecal composition described in terms of 5 broad diet categories for the period of hyperphagia. General interpretations of CANs are also given.

faced bear was a predator (Kurtén 1967), relationships between sizes of extant predators and their prey (Vezina 1985) lead to a prediction that the short-faced bear (335

Table 4. Species scores, eigenvectors of skull variables, and eigenvalues for the first 3 principal components (PC) from analysis of northern bear skulls. Skull variables are explained in the text and Fig. 1.

Parameters	PC1	PC2	PC3
Species			
Polar bear	-0.40	-1.04	-0.25
American black bear	-2.79	-0.33	-0.31
Asiatic black bear	-4.54	0.16	0.05
Brown bear—European	-0.49	-0.32	0.32
Brown bear—Pacific coastal	1.96	-0.32	0.34
Brown bear—continental	0.42	-0.06	0.29
Cave bear	3.77	0.16	0.36
Short-faced bear	3.19	0.28	-0.84
Giant panda	-1.11	1.47	0.03
Skull variables			
DENTA	0.317	0.735	0.224
CH	0.365	0.186	-0.111
MH	0.363	0.175	0.081
ZW	0.367	0.121	-0.070
FL	0.355	-0.313	0.370
ML	0.357	-0.328	0.229
CBL	0.355	-0.402	0.129
NW	0.346	-0.110	-0.848
Eigenvalues			
Proportion of variation	0.912	0.058	0.020

kg) preyed on animals as large as roughly 2200 kg, in the range of most mastodons (*Mammuthus americanum*) and smaller, presumably younger, woolly mammoths (*Mammuthus* spp.).

DISCUSSION

Diets of Extant Species

It is not altogether clear from this analysis the extent to which taxon alone, as opposed to prevailing environmental conditions, influenced what bears ate. Nonetheless, several expected patterns were evident. Asiatic and American black bears ate more mast than any other bear species, and when living in broadleaf forests, consumed relatively large volumes of hard mast. Small body sizes presumably allowed them access to tree mast in the face of intense competition from other frugivores (e.g., Bromlei 1965, Pelton 1982), while skull morphology of these same bears probably limited their use of foods such as roots, bamboo, and other graminoids that are more fibrous. Certainly, the contrast in food habits of Asiatic black bears with sympatric giant pandas and brown bears support this interpretation (Bromlei 1965, Schaller et al. 1989). Bears living in cold, open environments also ate the vertebrates and fibrous foods that were comparatively

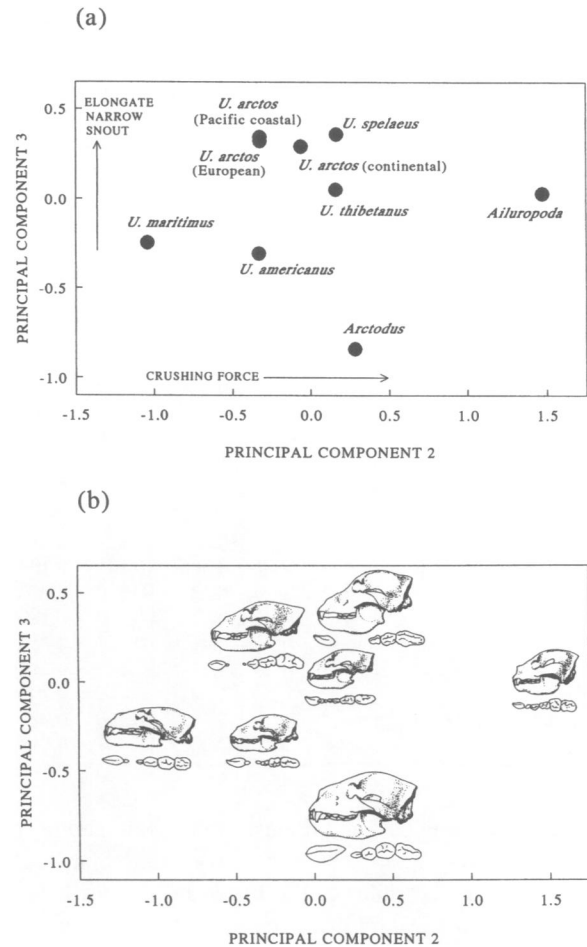


Fig. 3. Extant or recently extinct northern bear taxa are plotted with respect to the second and third principal components (PC2 and PC3) from analysis of skull measurements. (a) Functional or more general interpretations are shown for each PC as well as (b) skull profiles and planar views of the upper right dental row, shown proportional to their relative size. The 3 *Ursus arctos* subgroupings in (a) are represented by a simple skull in (b).

more abundant there. My analysis and Herrero (1978) strongly suggest that brown bears are better able to extract and process foods that are more fibrous, including roots, and thus are better adapted to living in non-forest environments. This interpretation is tenuously supported by the few investigations of sympatric American black and grizzly bears (e.g., Aune 1994), that have observed virtually no excavated foods in black bear feces in areas where excavated foods were a major part of the grizzly bear diet.

Brown bears are capable of living in temperate forests like those of eastern North America and eating a diet much like that of American black bears. This is clear from the

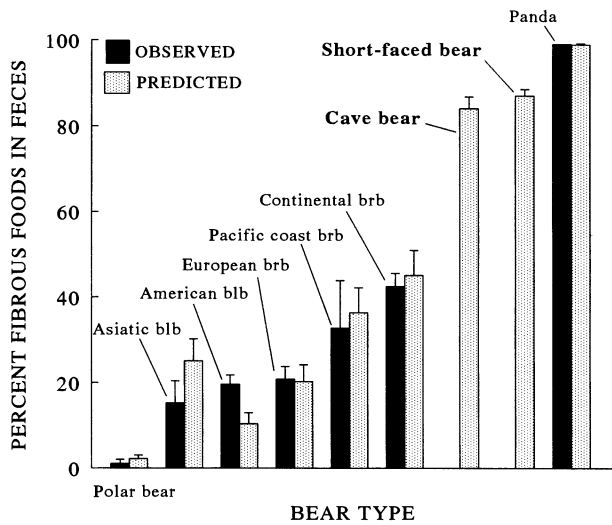


Fig. 4. Percent fibrous foods (foliage and roots) predicted in the feces of short-faced and cave bears are shown, based upon the relationship of fibrous foods to principal components from the morphometric analysis, as well as observed and predicted volumes of fibrous foods in feces of extant northern bears. Standard error bars are shown for observed and predicted values. Black bears are denoted by blb and brown bears by brb.

long history of brown bears living in pure or mixed broadleaf forests in Europe and by the extent to which diets of these bears overlapped with diets of American black bears. However, in contrast to Europe, temperate deciduous forests in North America and Asia are much more closely associated with black bears. It seems fruitful in the future to pursue the hypothesis that North American black bears, in combination with relatively high prime-

val densities of humans, were effective at competitively excluding brown bears under favorable environmental conditions; black bears via scramble competition and humans by direct mortality and interference competition. Asiatic black bears occupied Europe prior to the last glacial epoch (Erdbrink 1953a) and were probably prevented from reoccupying Europe from their Southeast Asian refuge because habitat bridges (i.e., contiguous temperate deciduous forests) did not develop across central Asia during the Holocene (Khotinsky 1984). Under these conditions, European brown bears would have had comparatively unimpeded access to expanding environments that might have otherwise favored black bears.

Diet and Morphology

Many features of skull and body morphology were associated with the diets of extant bears. A few of these associations were discussed in the previous section. This result does not contradict the expectation that body structure would shape as well as reflect food habits through a complex interplay of specific evolved physical adaptations, phenotypic plasticity, and longer-term evolutionary selection. In the short term, associations between diet and morphology likely rest upon developmental responses (e.g., hypertrophy) to mechanical forces (Moore 1965) and somatic adaptations that allow individual bear species to at least survive on, if not competitively use, certain foods. In either case, these relationships can be used to judiciously speculate about the food habits of extinct ursids as well as the niches of surviving bears.

Most variation in the skull morphology of extant bears is associated with the amount of fibrous foods in their diet. This association is plausibly interpreted in terms of

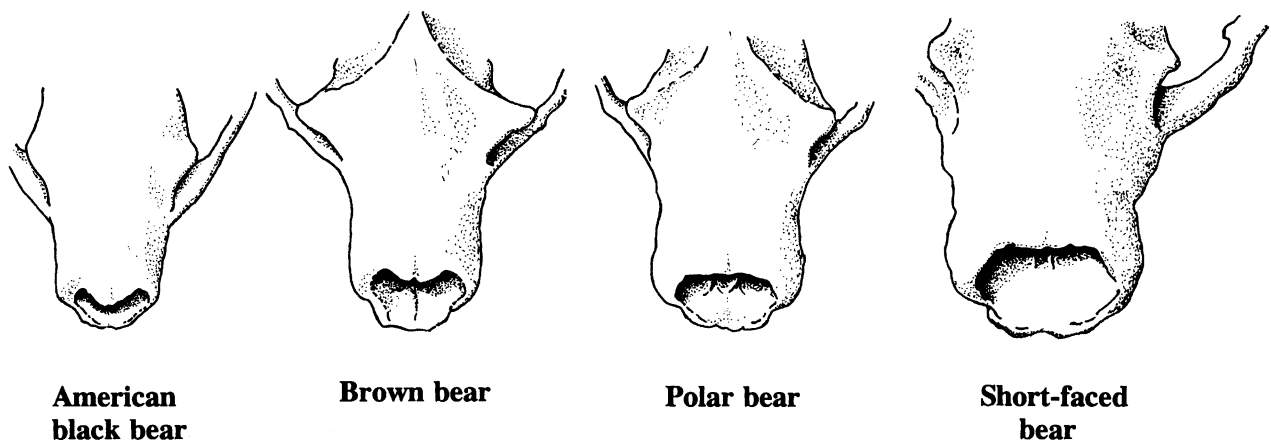


Fig. 5. Planar views of snouts are shown, emphasizing the nasal opening and bridge and rostral shape, from three representative extant bear species and the extinct short-faced bear.

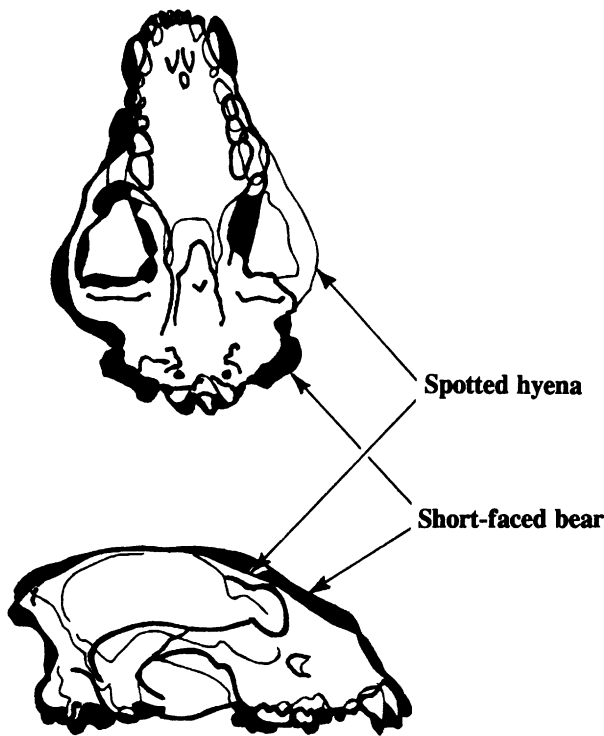


Fig. 6. Superimpositions of a short-faced bear (thick lines) and spotted hyena (thin lines) skull are shown, scaled to the same condylobasal length, in planar view and profile. Shading depicts areas of discrepancy between outlines of the 2 skulls.

adaptations that increase crushing capabilities — primarily through increases in dental crushing surface, accommodations for larger temporal and masseter muscles (i.e., increased zygomatic width and skull and mandible height), and configurations that bring the associated forces more effectively to bear on the occlusal plane. The gradient in snout shape, along with development of the diastema between canines and premolars, has less obvious functional interpretations.

An elongate and comparatively narrow snout is commonly interpreted as an adaptation to more selective feeding (Preuschoft et al. 1986, Gordon and Illius 1988, Greaves 1991). A diastema naturally arises from retention of crushing and grinding surfaces at the distal end of the dentary (Greaves 1991), nearer the zygoma where torsional stresses are decreased and the temporal muscles maximally effective (Preuschoft et al. 1986). A diastema between canines and premolars has also been associated with greater manipulation of vegetal foods within the mouth (Adrian et al. 1958). By either interpretation, this trend culminating in the cave bear is likely associated with increased use of the mouth to procure and further ma-

nipulate select fibrous vegetal foods. By contrast, a shorter rostrum combined with a broader nasal opening and retracted nasal bridge (epitomized by the polar and short-faced bears) implies several things—for one, a broader muzzle (Kurtén 1976), but more importantly, a rostrum that better resists the torsional forces associated with, and otherwise facilitates, grasping and manipulating large objects.

The substantial diastema of polar bears is inconsistent with the positive association of this feature with increased selection and manipulation of vegetal foods. Polar bears are almost strictly carnivorous. The diastema in this species is thus probably better understood in light of its recent derivation from the brown bear lineage (Kurtén 1964, Goldman et al. 1989, Shields and Kocher 1991) and the evolutionarily conservative nature of most dental features. It may simply be that the diastema in this species is an artifact of history and has no strong relationship to its present diet.

The Cave Bear

My results are consistent with previous hypotheses by researchers such as Erdbrink (1953*b*) and Kurtén (1976), and confirming evidence from analyses of carbon and nitrogen isotopes by Bocherens et al. (1994) that the cave bear ate a diet largely comprised of fibrous foods. Hilderbrand's (1996) analysis of isotopes suggests a more diverse diet, but is open to interpretation. Even so, the relatively simple ursid digestive tract (Jaczewski et al. 1960, Davis 1964, Mealey 1975), combined with the relatively short period of either low fiber content or above-ground availability typical at higher latitudes, make a diet comprised largely of foliage highly improbable. The panda accomplishes this feat aided by specific adaptations (e.g., 'the thumb') and the availability of a forage (bamboo) that is used by few competitors and has remarkably constant biomass and nutritional value throughout the year (Davis 1964, Schaller et al. 1985). A diet of leaves and stems is even more unlikely given the competition likely posed to grazing cave bears by the diverse fauna of larger herbivores in Pleistocene Europe (Kurtén 1968).

These complications can be reconciled with a fibrous vegetal diet by hypothesizing the cave bear to be a specialized root grubber. A root diet would be consistent with the extreme wear evident in cave bear teeth (Kurten 1958) and massive blunt claws well-suited (Hildebrand 1985) and previously hypothesized as adaptations to scratch digging (Erdbrink 1953*b*, Kurtén 1976). It would also fit the stout front limbs and powerful shoulder architecture of cave bears (Erdbrink 1953*b*, Kurtén 1976). This

Table 5. Body mass and indices of relative skeletal dimensions for northern bears and averaged for other carnivores by pursuit and ambush hunters (± 1 SD). Definitions and sources are given in footnotes.

Species or group	Mass (kg)	Skeletal indices ^a			
		FMT	VHR	RH	HW
Species					
Short-faced bear ^b	335	4.58	6.50	84.6	8.7
American black bear ^c	101	4.67	5.56	90.3	
Asiatic black bear ^d	86	5.30			
Brown bear ^c	178	4.75	5.76	88.6	9.3
Cave bear ^f	284	4.83	5.51	75.6	10.5
Polar bear ^g	288	5.30	5.03		
Giant panda ^h	125	9.13	5.06	77.1	9.4
Group					
Pursuit hunters ⁱ	34 \pm 17	2.40 \pm 0.1	5.96		
Ambush hunters ⁱ	37 \pm 39	2.59 \pm 0.3	4.56 \pm 0.3		

^a FMT = femur length/length of longest metatarsal; VHR = humerus + radius length/length of thoracic vertebrae 10 + 11 + 12; RH = radius length/humerus length as %; HW = narrowest width of humerus shaft/humerus length as %.

^b Kurtén (1967), Emslie and Czaplewski (1985).

^c Davis (1964), Emslie and Czaplewski (1985), Van Valkenburgh (1985).

^d Bromlei (1965), Van Valkenburgh (1985).

^e Erdbrink (1953b), Davis (1964), Kurtén (1967), Emslie and Czaplewski (1985), Van Valkenburgh (1985).

^f Erdbrink (1953b), Kurtén (1967).

^g Van Valkenburgh (1985).

^h Davis (1964).

ⁱ Davis (1964), Van Valkenburgh (1985).

latter feature has been associated with fixing the scapula in resistance to pulling forces along the long axis of the fore-limbs (Davis 1949), more specifically among grizzly bears as an adaptation to digging (Herrero 1978, Craighead and Mitchell 1982).

The cave bears' large diastema would be consistent with the root-grubbing hypothesis. The diastema appears to be associated with manipulation of both *Hedysarum* (*Hedysarum* spp.) and yampah (*Perideridia gairdneri*) when grizzlies are consuming roots of these plants (pers. obs.). Cave bears may have had access to many large starchy-rooted species, such as *Hedysarum* spp. and *Conopodium majus*, that are common in boreal, arctic, and alpine regions of present-day Eurasia (Komarov 1948, Couturier 1954). It is also possible that some of the numerous ancestral or surviving Eurasian species of pika (*Ochotona* spp.), ground squirrel (*Spermophilus* spp.), and marmot (*Marmota* spp.) would have been available to and used by a cave bear that specialized in scratch digging.

This possible reliance on roots and other fibrous foods provides additional context for understanding the cave bears' extinction. First, this type of diet would be consistent with the very low reproductive rate postulated by Kurtén (1958), similar to that observed for the herbivorous panda (Schaller et al. 1985). Although large body size could partly explain low fecundity, this relationship

does not automatically follow from greater body mass. Lower fecundity and more specialized food habits predictably would have made cave bears vulnerable not only to a rapidly changing landscape, but also to the competition and possible added mortality brought by the advent of 2 generalist omnivores (brown bears and modern humans) in Europe during the late Pleistocene. Arrival of modern humans about 30,000 years ago could have tipped the scale against cave bears in what may have been an already stringent competitive triangle that included Neanderthals (*Homo sapiens neanderthalensis*) and recently arrived brown bears. In any case, these results are consistent with the hypothesis that humans were an important catalyst in the demise of cave bears (Erdbrink 1953b, Kurtén 1976).

The Short-Faced Bear

Kurtén (1967) and Emslie and Czaplewski (1985) offer strikingly different hypotheses about the food habits of short-faced bears. Kurtén (1967) evoked an active predator that could achieve comparatively high speeds (for a bear) because of relatively long legs and forward-aligned feet. He also speculated that the broad rostrum and short face and neck facilitated grabbing and subduing prey, complemented by features of the lower first molar that aided meat consumption. By contrast, Emslie

and Czaplewski (1985) hypothesized that short-faced bears were omnivores, if not near-exclusive herbivores. Their argument rested principally on the species' large body mass (the short-faced bear is larger than any extant carnivore and comparable in size to some herbivores) and alternate explanations for features that Kurtén (1967) had associated with carnivory.

The results presented here contribute to judging the relative merits of these contrasting views. An uncritical extrapolation of the relationship between fibrous foods and skull morphology of extant bears predicts that short-faced bears ate an almost wholly fibrous diet. Yet if this were so, the bear's broad rostrum, broad incisor arcade and short face suggest a relatively unselective diet of coarse foliage (Hylander 1975, Gordon and Illius 1988, Janis and Ehrhardt 1988). As with the cave bear, this is highly unlikely given the simple ursid digestive tract and the abbreviated season of high forage quality at northerly latitudes. Moreover, the short-faced bear's long legs and short neck (Kurtén 1967) would have complicated ground-level grazing, unless this species filled the browsing niche. More likely, the apparent crushing capabilities of its skull facilitated foraging behavior other than grinding roots (Kurtén 1967, Emslie and Czaplewski 1985) or foliage.

Emslie and Czaplewski (1985) also suggested that the short-faced bear's tall and slender stature (1.0–1.5 m at the shoulder) may have been either an adaptation to scanning over tall ground cover or a possible means of procuring foliage and berries from the limbs of trees and shrubs. It is hard to imagine what benefits would be derived for these purposes in the Beringian steppe-tundra or when most ground cover during the late Pleistocene of modern-day western United States was likely <1 m tall (Thompson and Mead 1982). In any case, a bear that browsed flowers, foliage, seeds, or berries from the canopies of trees and shrubs would have almost certainly been severely handicapped by a rostrum and incisor arcade as large and as flattened as that of the short-faced bear (Hylander 1975, Gordon and Illius 1988, Janis and Ehrhardt 1988). Again, presumed adaptations to either herbivory or frugivory fail to give a satisfactory explanation of the short-faced bear's body proportions.

Emslie and Czaplewski (1985) further contend that large body size is evidence against carnivory. Several authors (e.g., Rosenzweig 1968, Hespeneide 1975, Vezina 1985) have observed a relatively strong positive relationship between the size of solitary predators and their prey. Larger prey presumably allow for the existence of larger predators. Large body size would therefore only be a convincing argument against carnivorous short-faced bears if there were no commensurate-sized

prey in Pleistocene North America. In fact, a number of large herbivores existed, including mastodons, mammoths, and bison (*Bison* spp.; Kurtén and Anderson 1980), that could have constituted the prey of a predator as large as the short-faced bear (see Results). It seems more than coincidence that the largest short-faced bears (*A. s. yukonensis*) shared Pleistocene Alaska with some of the highest North American mammoth concentrations (Agenbroad 1984). Large body size is not an inherently strong argument against carnivory, and in this case may even be an argument for it.

Carnivorous food habits still provide the most consistent and compelling explanation for diagnostic features of short-faced bear morphology and are also consistent with the constraints of a simple ursid digestive tract. This interpretation is furthermore consistent with previously observed associations of short-faced bear remains and herbivore bones marked and fragmented in ways characteristic of bear scavenging (Agenbroad and Mead 1986, Voorhies and Corner 1986, Guthrie 1988, and Gillette and Madsen 1992) and with analysis of stable carbon and nitrogen isotopes from bone collagen (Matheus 1995).

Skeletal indices suggest a relatively mobile bear (Van Valkenburg 1985, Garland and Janis 1993) that, like many other species, perhaps achieved this performance in spite of an array of unique phylogenetic traits (e.g., a plantigrade or semi-plantigrade posture; Taylor et al. 1974, Garland and Janis 1993). The skull exhibits features that, along with the short neck, are plausibly interpreted as adaptations to grasp, kill, and dismember prey, probably in concert with the characteristically flexuous ursid paws. If this bear engaged in ambush-type predation, it would likely have been swift enough to catch its large-bodied prey, perhaps grasping it from the rear with its paws and collapsing the hind-quarters with a combination of weight and a crippling bite to the back, much like contemporary brown bears. A skull in many respects strikingly similar to that of the spotted hyena may have furthermore aided a short-faced bear's manipulation and dismemberment of a very large carcasses that it had obtained.

If the short-faced bear were adapted to prey on or scavenge very large herbivores, then its' late-Pleistocene extinction is comparatively easy to understand. Most likely, the short-faced bear went extinct because its primary food went extinct (McDonald 1984, Owen-Smith 1987). Kurtén and Anderson (1974, 1980) suggested that competition with newly arrived brown bears was a major cause. In contrast, Matheus (1995) and results presented here suggest that there would have been relatively little niche overlap between the 2

species and that brown bears probably played a relatively minor role in the short-faced bears' extinction; perhaps simply hastening its demise through scramble competition for carrion of smaller-bodied herbivores.

Matheus (1995) hypothesizes that short-faced bears were primarily scavengers, discounting their potential role as predators. Whereas the results presented here do not constitute evidence for or against this proposition, it is worth reflecting on the food habits of 2 other species, spotted hyenas and brown bears, that, when eating meat, are conventionally deemed to be scavengers. In particular, field studies have shown that, even though their physical form is consistent with scavenging, these species can be formidable predators and can, in fact, derive much of their meat from kills (Kruuk 1972, Mattson 1997). I therefore argue for caution against over-interpreting behavior from physical form.

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Appendix 1. Untransformed values for morphometric variables used in principal components analysis of northern bear skulls. Acronyms are explained in Fig. 1 and the text; sources are given in footnotes.

Species	Body mass (kg)	CBL (mm)	CH (mm)	FL (mm)	ML (mm)	MH (mm)	ZW (mm)	NW (mm)	DENTL (mm)	DENTA (mm ²)
Giant panda ^a	125	249	114	80	174	102	197	42	75	1613
Asiatic black bear ^b	86	212	80	59	155	68	136	30	57	707
American black bear ^c	101	257	90	78	170	80	149	42	57	768
Brown bear—European ^d	141	307	107	108	221	92	193	46	67	1145
Brown bear—continental ^e	148	324	123	110	233	110	207	49	75	1288
Brown bear—coastal ^f	277	377	132	130	271	132	252	57	82	1420
Cave bear ^g	248	430	168	153	301	146	292	68	97	2194
Polar bear ^h	288	331	112	103	222	96	199	52	60	790
Short-faced bear ⁱ	335	380	160	125	274	137	289	88	86	1891

^a Davis (1964).

^b Ognev (1931), Pocock (1933), Bromlei (1965).

^c Erdbrink (1953a), Davis (1964), Erickson et al. (1964), Bunnell and Tait (1981), Pelton (1982).

^d Ognev (1931), Erdbrink (1953b), Kurtén (1955, 1964), Krott (1962), Novikov et al. (1969).

^e Ognev (1931), Rausch (1951, 1953), Davis (1964), Yoneda and Abe (1975).

^f Ognev (1931), Rausch (1953), Davis (1964), Yoneda and Abe (1975).

^g Kurtén (1955, 1958, 1964, 1967, 1976).

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ⁱ Kurtén (1967).

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