

FORAGE DIGESTIBILITY AND FITNESS IN GRIZZLY BEARS

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Abstract: Abilities to digest dry matter, crude protein, and gross energy were evaluated for 2 captive grizzly bears (*Ursus arctos*) in 1977 and 1978. Four diets were used: 1 basal (horsemeat plus dog chow), 2 incorporating natural foodstuffs (blueberries and salmon), and 1 containing high fiber (beet pulp). Average apparent digestibilities (% dry weight) for the horsemeat plus dog chow, blueberry, and salmon diets were 82% (dry matter), 90.2% (crude protein), and 88.1% (gross energy). Relative digestibilities of specific foodstuffs in descending order were: blueberries, salmon, and beet pulp. Addition of beet pulp to the diet reduced measured digestibilities to: 48.7% (dry matter), 75.1% (crude protein), and 62.0% (gross energy). Grizzly bears feeding on horsemeat exhibited digestibilities similar to those reported for obligate carnivores. Although *U. arctos* has evolved omnivorous food habits and morphological adaptations for herbivory, it digests cellulose poorly but has apparently conserved the ability to digest meat efficiently. The ability to digest high quality forage rapidly is presumably a necessary concomitant of denning.

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Optimal foraging theory commonly assumes that animals increase fitness by maximizing net rate of energy intake (e.g. Schoener 1971, Werner and Hall 1974, Charnov 1976a, b; Pyke et al. 1977). In their review, Bunnell and Tait (1981) noted that age of first reproduction, litter size, and interval between breeding each appeared influenced by nutrition among brown bears, black bears (*U. americanus*), and polar bears (*U. maritimus*). The profound influence of nutrition on the number of progeny and their survival suggested that bears could increase fitness by maximizing net rate of energy intake, possibly by selecting highly digestible forage.

In North America, food habits of *U. arctos* have been assessed for populations in Wyoming (Graham 1978, Mealey 1975, 1980), British Columbia (Mundy 1963, Hamer 1974, Lloyd and Fleck 1978), Alberta (J.D.W. Hamer et al., unpubl. mss., Parks Can., Calgary, Alberta, 1977, 1978; J.A. Nagy and R.H. Russell, unpubl. annu. rep., Can. Wildl. Serv., 1978), Yukon Territory (Pearson 1975), and Alaska (Murie 1944, Chate-lain 1950, Clark 1957). Observations are also available for Eurasian populations (e.g., Haglund 1968, Kistchinski 1972, Zunino and Herrero 1972). These studies reveal dramatic seasonal shifts in the diet of grizzly and brown bears. Mealey (1980) estimated digestibilities of foodstuffs by comparing proximate analyses (Cramp-ton and Harris 1969) of food items with scats containing residues of the same items collected at feeding sites. Little additional work has been done to document the bears' ability to extract en-

ergy and nutrients from food consumed. Those abilities may indicate reasons for dietary shifts.

This study was designed to quantify the ability of the coastal grizzly bear of British Columbia to digest specific forage items. Objectives were: to document apparent digestibilities of dry matter, crude protein, and gross energy by grizzly bears; to document relative digestibilities of specific natural food types, e.g., blueberries and salmon; and to consider those data in terms of fitness of grizzly bears.

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METHODS

In the spring of 1977, 2 yearling grizzlies (male and female) were captured at Wakeman Sound, B.C. (about 51°N, 126°30'W) and transported to the Animal Care facilities of the University of B.C. The bears were "nuisance" bears at the dump of a logging camp. At time of capture, the male weighed 90 kg and the female 75 kg.

The bears were maintained on a basal diet of 50% horsemeat and 50% Purina dog chow on a

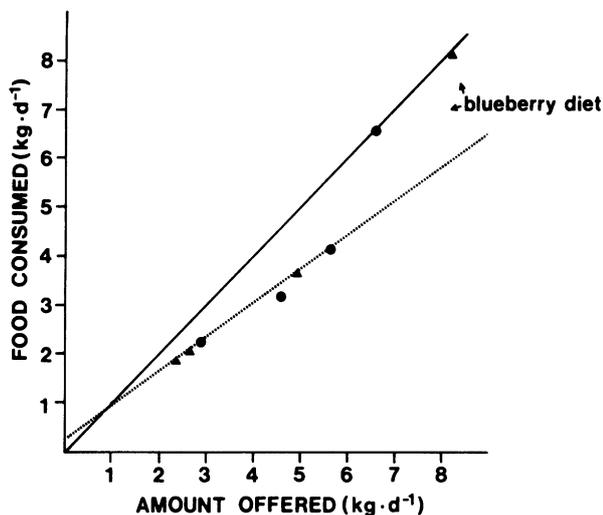


Fig. 1. Food consumed by grizzly bears as a function of amount offered (circles = male; triangles = female). Solid line illustrates a 1:1 relationship, dotted line illustrates the observed relationship.

dry weight basis. They were exposed to experimental diets never less than 5 days before trials. Specific forage types were evaluated by addition to the basal diet. Trials lasted 10 days. The basal diet contributed 50% (moist weight) of the entire diet during trial periods. Forage types evaluated were blueberries (*Vaccinium corymbosum*), coho salmon (*Oncorhynchus kisutch*), and beet pulp. Diets were mixed with a 20 hp screw-type meat grinder and paddle-type mixer. Bears were fed weighed samples twice daily (0800 and 1700) during each trial. The amount of food on offer varied with food type (Fig. 1). The basal diet was also fed to 4 juvenile dogs.

Three feed samples were collected from each diet: at the time of mixing, at day 5 of the trial, and at the end of the trial. Individual components of the diets were analyzed. Fecal samples were collected on days 5, 7, and 10 of each trial, 1 sample per animal. All samples were frozen and subsequently dried in a forced-air convection oven, and dry matter was determined for feeds and feed components. Fecal samples were machine-ground (mesh-size 20), but the high fat content of most feed samples necessitated hand-grinding with mortar and pestle. Nitrogen contents were estimated by the macro-Kjeldahl technique (A.O.A.C. 1970). Gross energy content was estimated by Gallenkamp adiabatic oxygen bomb calorimeter. Acid detergent fiber (ADF),

Table 1. Composition of experimental diets fed to captive grizzly bears and domestic dogs at the University of British Columbia, 1977-78 (\bar{X} of 3 to 6 replicates).

Diet	Composition on basis of dry matter			
	% dry matter	Crude protein (g/100g)	Gross energy (cal/g)	% AIA ^a
Basal (bears)	50.1	36.3	5577	0.11
Basal (dogs)	49.4	36.4	5742	0.09
Basal and blueberries	34.3	31.7	5498	0.38
Basal and salmon	32.4	53.0	5529	0.10
Basal and beet pulp	49.7	21.2	4729	1.42

^a Acid-insoluble ash

a measure of lignocellulose content, was estimated for plant components using the technique of Waldern (1971). Values of acid insoluble ash in feed and feces were assessed by the technique described by McCarthy et al. (1974) and Van Keulen and Young (1977).

Calculations of apparent digestibility employed equations (1) and (2):

$$\% DMD = 1 - \left(\frac{\%AIA \text{ in feed, dm}}{\%AIA \text{ in feces, dm}} \right) 100 \quad (1)$$

where %DMD = apparent percent of dry matter digestible, %AIA = percent acid-insoluble ash on a dry-matter (dm) basis, and Y = specific nutrient treated.

% nutrient digestible

$$= 1 - \left(\frac{\%AIA \text{ in feed} \times \%Y \text{ in feces}}{\%AIA \text{ in feces} \times \%Y \text{ in feed}} \right) 100 \quad (2)$$

RESULTS

With the exception of the blueberry diet, bears consumed an average of $70 \pm 4\%$ of the food offered them (Fig. 1). The proportion of food rejected was remarkably consistent over the range of food offered (Fig. 1). Blueberries were avidly consumed; the small portion rejected ($< 1\%$) may have resulted from difficulties by the bears in handling the forage.

Upon termination of the trials, the male weighted 210 kg and the female 172 kg. Weight

Table 2. Fecal analyses of a male and a female captive grizzly bear and 4 dogs fed experimental diets at the University of British Columbia, 1977-78 (\bar{X} of 4 to 8 replicates).

Diet	Animal	Composition on basis of dry matter		
		Crude protein (g/100g)	Gross energy (cal/g)	% AIA
Basal	Male	21.6	3710	0.73
	Female	21.1	3827	0.54
Basal and blueberries	Male	19.7	3874	2.34
	Female	21.5	4114	2.49
Basal and salmon	Male	23.8	3499	0.43
	Female	22.2	3086	0.50
Basal and beet pulp	Male	10.4	3669	2.85
	Female	10.2	3342	2.70
Basal	Dogs	27.2	4408	1.11

gains were 0.63 kg/day for the male and 0.51 kg/day for the female.

The basal diet offered bears and dogs did not differ significantly (Table 1). The blueberry and salmon diets were significantly lower than the basal diet in percent dry matter (t -test, $P < 0.001$). All three experimental diets differed from the basal diet in crude protein ($P < 0.001$). Only the beet pulp diet differed significantly from the basal diet in gross energy ($P < 0.002$). Fecal analyses of animals on known trial diets (Table 2) should prove useful to field workers estimating digestibilities by the technique of Mealey (1980).

Equations 1 and 2 were used to estimate the digestibilities of dry matter, crude protein, and gross energy (Table 3). When feeding on the basal diet, domestic dogs showed greater digestibilities of dry matter, crude protein, and gross energy than did bears (Table 3). Most differences were statistically significant according to t -tests: dry matter, $P < 0.01$; crude protein, $P < 0.02$; gross energy, $P < 0.06$.

Estimates of digestibility of individual forage types were derived using the data of Table 3. Consider estimation of the digestibility of blueberries by the male grizzly. Composition of the trial diet on a dry weight basis was 75.5% basal and 24.5% blueberries. The estimated dry matter digestibility by the male was 85.4% while feeding on the basal diet and 83.6% while feeding on the blueberry plus basal diet (Table 3). An estimate of his ability to digest blueberries, Y , is obtained from the relationship:

Table 3. Apparent digestibilities of dry matter, crude protein, and gross energy by a male and a female captive grizzly bear and 4 domestic dogs fed experimental diets at the University of British Columbia, 1977-78.

Diet	Animal	Apparent digestibility (% dry weight)		
		Dry matter	Crude protein	Gross energy
Basal	Male	85.4	91.3	90.3
	Female	80.1	88.4	86.3
Basal and blueberries	Male	83.6	89.8	88.5
	Female	84.6	89.5	88.5
Basal and salmon	Male	77.6	89.9	85.8
	Female	80.8	92.0	89.3
Basal and beet pulp	Male	50.1	75.5	61.3
	Female	47.3	74.7	62.7
Basal	Dogs: mean	91.7	93.9	93.5
	range	90.8-92.3	93.2-94.2	92.9-94.2

$$0.755 (0.854) + 0.245 Y = 0.836 \quad (3)$$

Thus, $Y = 0.78$, or 78%. Digestibilities of individual forage types were estimated using the formulation of equation 3 (Table 4).

DISCUSSION

Over the 190-day trial period, increases in body weight were 133% and 129% for the male and female respectively. Nagy and Russell (unpubl. annu. rep., Can. Wildl. Serv., 1978) reported weight gains of 330% over 148 days for an immature 2-year-old male grizzly bear and 91% over 90 days for an immature female. Daily weight gains were 0.39 and 0.36 kg/day for the male and female respectively. From data of Pearson (1975) we calculated rates of weight gain for 2 grizzly bears in southwest Yukon: 0.41 kg/day over 126 days for an adult male and 0.64 kg/day over 16 days for a 2-year-old female that fed intensively on berries of *Shepherdia canadensis*. Rates of weight gain for our captive grizzly bears

Table 4. Dry-matter digestibilities of specific dietary components by a male and a female captive grizzly bear at the University of British Columbia, 1977-78.

Dietary component	Dry-matter digestibility (% dry weight)		
	Male	Female	Mean
Blueberries	78.3	98.5	88.4
Salmon	65.2	82.1	73.6
Beet pulp	12.0	10.9	11.5

Table 5. Interspecies comparison of ability to digest dry matter, protein, and gross energy from various diets.

Species and data source	Food item(s)	Apparent digestibility (% dry weight)		
		Dry matter	Crude protein	Gross energy
<i>Ursus arctos</i> (this study)	Mean of basal, blueberry, and salmon diets	82.0	90.2	88.1
<i>Ursus arctos</i> (this study)	Basal plus beet pulp	48.7	75.1	62.0
<i>Ursus arctos</i> (Mealey 1975)	Cervidae and Bovidae	81.3		
<i>Ursus arctos</i> (Mealey 1975)	<i>Salmo clarki</i>	73.2		
<i>Ursus arctos</i> (Mealey 1975)	Succulent herbs		42.8	
<i>Ursus maritimus</i> (Best 1975)	<i>Phoca hispida</i>	82.0	83.2	91.8
<i>Canis familiaris</i> (this study)	Basal diet (horsemeat and dog chow)	91.7	93.9	93.5
<i>Lynx rufus</i> (Golley et al. 1965, Morris et al. 1974)	Chicken, deer, rabbits and Zu/Preem ^a	79.0	90.4	91.0
<i>Panthera tigris</i> (Morris et al. 1974)	Zu/Preem	79.2	88.8	
<i>Felis concolor</i> (Morris et al. 1974)	Zu/Preem	80.1	92.1	
<i>Taxidea taxus</i> (Jense 1968, Morris et al. 1974)	Zu/Preem	77.1	88.1	86.5

^a Zu/Preem = commercial preparation based on horsemeat and meat byproducts

(0.51 and 0.63 kg/day) appear similar to rates documented for free-ranging grizzly bears (see also Kingsley et al. 1983). The capacity for rapid weight gain is likely a necessary concomitant of the denning habit, which annually enforces a 4- to 7-month period of inactivity.

Digestibilities of dry matter and crude protein by *U. arctos* differed little from digestibilities recorded for obligate carnivores (Table 5). Morris et al. (1974) presented data for 13 felid species (obligate carnivores); they found mean digestibilities in these species for dry matter and crude protein of 78.8% and 89.6% respectively. These calculated digestibilities for felids were lower than those reported for *U. arctos* (Table 5). Where it can be evaluated statistically, digestibility of gross energy did not differ between *U. arctos* and obligate carnivores ($P > 0.05$). *Taxidea taxus*, more omnivorous than the Felidae, exhibited slightly lower digestibilities of meat than *U. arctos*.

Ursidae is the youngest Family within Order Carnivora (Colbert 1969). The *Ursus* line can be traced to *Ursavus elmensis* of the Miocene (Kurtèn 1976). Over the subsequent 20 million years, broad trends in evolution are evident towards larger body size, reduction of cheek teeth, expansion of the molars' chewing surface, and longer claws. Within *U. arctos* several trends are clearly associated with increased herbivory, particularly those in dentition and the claws (Herrero 1978, Bunnell and Tait 1981). Despite these long-lasting evolutionary trends towards herbivory, and the large vegetative component in diets of grizzly bears, digestive capabilities of *U. arctos* are similar to those of obligate carnivores (Table 5).

Adaptations of *U. arctos* towards herbivory do not include the capacity to digest coarse forage efficiently. Blueberries with 15% acid-detergent fiber (ADF) are highly digestible (88.4%, Table 6). Dry-matter digestibility of the more fibrous

beet pulp (46.1% ADF) is much lower (11.5%, Table 6). The depressive effect of ADF components, particularly lignin, is well documented for ruminants (Schoonveld et al. 1974, Short et al. 1974). Among monogastric pigs (nonruminants), an increase in crude fiber within the diet only slightly affects its digestibility coefficient, but markedly depresses the digestibility of the rest of the diet (Rerat 1978). Within *U. arctos* an increase in dietary fiber dramatically decreases the apparent digestibilities of fiber, dry matter, and gross energy. Digestibility of crude protein is depressed, but not as markedly (Table 6).

U. arctos and *U. americanus* have unspecialized digestive systems, essentially a carnivore's digestive system which has been lengthened (David 1964). Unlike many other nonruminant omnivores, they have no caecum and their stomachs are too acid to encourage the microflora and microfauna needed for digestion of cellulose (Rogers 1976). *U. maritimus* has returned to carnivory only recently. Fossil records of *U. maritimus* do not date earlier than 70,000 B.P., and distinct changes towards more carnivorous dentition have occurred in the last 10,000 years (Kurtén 1964, 1976). Despite the recent evolution of more carnivorous dentition and almost purely carnivorous food habits (Lønø 1970, Russell 1975), the digestive capabilities of *U. maritimus* differ little from those of the omnivorous *U. arctos* (Table 5).

The fossil record, present anatomy, and documented digestive capabilities (Tables 3 through 6) suggest that evolution of digestive capabilities has been conservative in *U. arctos*. While some morphological adaptations towards herbivory (teeth and claws) are pronounced, grizzly bears digest fibrous vegetation poorly. Other species can increase fitness by maximizing rates of net energy gain (e.g., Krebs et al. 1974, Huey and Slatkin 1976, Stenseth 1978). Bunnell and Tait (1981) reported that age of first reproduction, mean litter size, and breeding interval of grizzly bears were influenced by diet. We thus suppose that selection pressures operating on *U. arctos* have encouraged means of enhancing energy intake. Present results of these pressures are omnivorous food habits, morphological adaptations for herbivory, and a well conserved ability to digest meat.

Table 6. Apparent digestibilities by two grizzly bears of acid-detergent fiber, dry matter, crude protein, and gross energy in diets of different fiber content, University of British Columbia, 1977-78.

Diet or dietary component	Acid detergent fiber (%)	Apparent digestibility (% dry weight)			
		Acid detergent fiber	Dry matter	Crude protein	Gross energy
Blueberries	15	83.4	88.4	89.1	89.1
Basal diet	n.d. ^a	n.d.	82.7	89.9	88.3
Beet pulp	46.1	4.8	11.1	58.7	29.7

^a No data, ADF not measured for basal diet, assumed intermediate between blueberries and beet pulp.

It is unclear how ancient the denning habit is within the *Ursus* line. Fossils of the source of the line, *Ursavus elmensis*, were found in a rock crevice dating from the Miocene; North American ursid fossils more than a million years old have been recovered from caves. For most current grizzly bear populations, the period of rapid weight gain necessary for effective reproduction occurs shortly before denning. Most vegetation is then becoming more fibrous and less digestible; fruits are an exception. Presumably both denning and digestive capabilities were part of the fitness set encouraged by natural selection. Denning is an adaptation to at least two phenomena: (1) the production of small, near-naked young unable to thermoregulate, and (2) marked seasonal changes in food availability.

The first phenomenon appears to exert stronger control. Subtropical species of Ursidae den for shorter periods in less sheltered locations than does *U. arctos*, and males in southern populations of *U. americanus* and *Selenarctos thibetanus* do not den every year (Bunnell 1981). Adult male *U. maritimus* also do not den, but they are carnivorous and less constrained by the second potential control, food availability. Rapid digestive capabilities and rapid weight gain prior to denning are required for denning to be a viable strategy. If physiological capabilities to digest foods low in fiber are more rapid and different from those appropriate to digesting foods high in fiber, we expect the former to be encouraged or conserved in grizzly bears. Grizzly bears apparently have enhanced their fitness by evolving morphological adaptations to herbivory and conserving physiological adaptations to carnivory. *U.*

arctos are committed to seeking forage of relatively high quality, a pattern broadly evident in the studies of food habits cited and previously noted by Herrero (1978). Together these observations document the importance to grizzly bears of habitats containing succulent forage (e.g., riparian areas, avalanche chutes).

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