

GRIZZLY BEAR FOOD AND HABITAT IN THE FRONT RANGES OF BANFF NATIONAL PARK, ALBERTA

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Abstract: Food and habitat used by grizzly bears (*Ursus arctos*) in the Front Ranges of Banff National Park were studied during 1976–80 using fecal analysis, feeding site examination, direct observation, and radio-tracking. Important foods included pink hedysarum (*Hedysarum alpinum*) roots, yellow hedysarum (*H. sulphurescens*) roots, bearberries (*Arctostaphylos uva-ursi*), graminoids, horsetails (*Equisetum arvense*), buffaloberries (*Shepherdia canadensis*), and *Vaccinium* spp. fruits. Most foods were eaten in dry meadows, shrubfields, or open forest. Horsetails were the only notable exception; many feeding sites occurred in mature forest. The alpine zone was unimportant as feeding habitat. Seasonal changes in diet and habitat use appeared to be related to phenology with bears eating plant parts which seemed to be at nutritious development stages. Hedysarum roots, the bears' major food, had significantly less crude protein and more fiber when plants were flowering than when they were in pre-leaf. Related to this, digging by bears was minimal during the mid-summer flowering period. Seasonal habitat use also appeared to be influenced by hedysarum phenology. As the spring digging season progressed, hedysarum diggings occurred more on north-facing slopes and at higher elevations, where phenology was retarded. Later-season root digging was inversely related to buffaloberry abundance: the volume of roots in feces during August–October was greater in 1976 and 1978, 2 years when buffaloberry abundance was significantly lower than in 1977 or 1979. We concluded that buffaloberries, known to be high in soluble carbohydrate, were preferred over hedysarum roots. During summer, grizzly bears ate horsetails in sites where the plants were in immature, nutritious development stages. The elevation of horsetail feeding sites was significantly higher in late July–August than in early July. Grizzly bears thus ate food high in soluble nutrients and low in fiber by making seasonal changes in both the food and habitat they selected.

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This research documents the food habits and habitat use of grizzly bears in the Cascade and Panther valleys of Banff National Park. In addition, we have tried to understand why grizzly bears switched from 1 food to another, or moved from 1 habitat type to another. The quality, quantity, and availability of food at certain seasons or in certain habitat types were the variables considered in these analyses.

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STUDY AREA

The study area occupies approximately 250 km² in the eastern slopes of Banff National Park, within the Front Ranges of the Rocky Mountains (Fig. 1). The continental divide is 45 km to the west.

Glaciation has developed a gentle U shape to the study area's larger valleys, which run northwest-southeast in major faults. Numerous smaller drainages dissect the intervening mountain blocks which, in conjunction with the moderate relief (elevations range from 1,600 to 3,000 m), result in a complex juxtaposition of slopes with differing aspects, elevations, and steepness. Abrupt changes regularly occur within 2–3 km or less of any 1 point in the study area.

The Front Ranges are separated from the Pacific Ocean by the Coastal and Columbia mountains and by the main ranges of the Rocky Mountains. As a result, the climate in the study area is essentially continental. According to extrapolations by Janz and Storr (1977:325), certain portions of the main valleys likely are semiarid (< 50 cm precipitation/year). This rainshadow effect is exacerbated by the drying effect of the warm, westerly, chinook (foehn) winds that characterize the Rocky Mountains east of the continental divide. Many southeast- through west-facing slopes (135°–270°) are forest-free below the normal treeline, in part because of low precipitation and the drying influence of strong chinook wind.

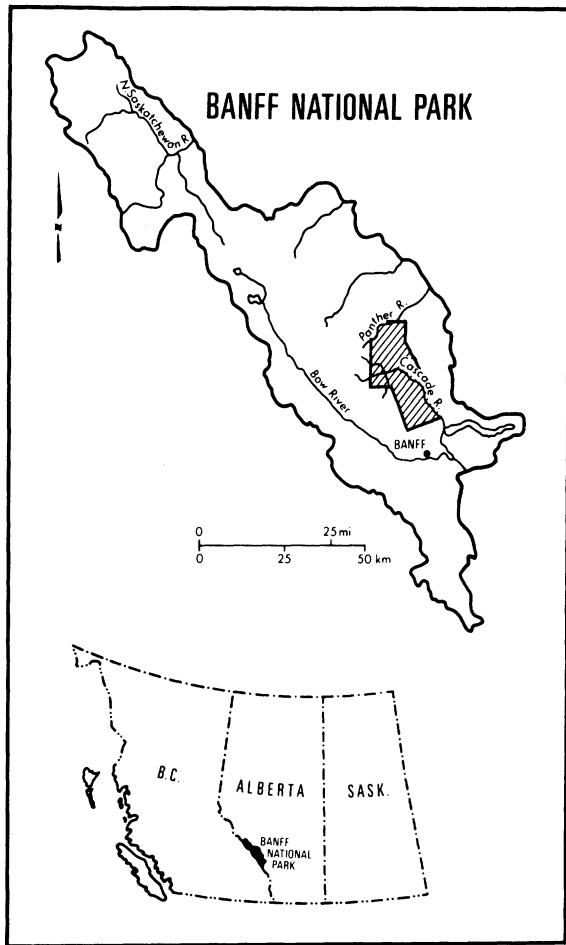


Fig. 1. Study area location.

The subalpine zone of the study area is dominated by coniferous forest. Groves of *Populus* spp. cover less than 1% of the area. Overall, forest covers about 60% of the core study area. Table 1 briefly describes major vegetation types. Additional detail is available in Holland and Coen (1983) and Hamer (1985).

We did not determine grizzly bear population size during this study, but we did count recognizable, unmarked grizzly bears. During 1976–77, we identified 23 recognizable grizzly bears in a core study area (approximately 150 km²). During 1976–80, we identified 5–7 family groups whose home ranges included at least part of the study area. The total number is bracketed as 5–7 because 4 of the groups likely included only 2 adult females accompanied by consecutive litters of cubs. The coat colors and sighting locations suggested these were the same adult females,

as did the ages of the cubs (i.e., in predicted phases for consecutive litters).

METHODS

During the 1976–80 period, 945 man-days were spent in the field. Grizzly bear feeding sites were located and examined, and when possible, bears were observed directly. Feces were collected for food item determination. During 1978–80, 2 adult female grizzly bears were radio-tracked as a means of facilitating data collection. Recognition of grizzly bear feces and signs was greatly simplified by the absence of black bears (*U. americanus*) in the study area (Hamer et al. 1981).

Searches for signs of feeding activity and feces were made off-trail while traveling cross-country. This procedure was possible because of the study area's easy traveling conditions. Alders (*Alnus* spp.) or other thicket-forming species were absent; lush, tall herb communities were sparsely stocked, of low stature (approximately 1 m tall), and uncommon in the area; and heavily stocked, windfall-obstructed, mature forests were almost absent. These conditions contrast with moister environments, where lush vegetation can prevent easy off-trail movement, obscure signs of feeding, and visually hinder the collection of fecal samples (contrast Hamer 1974, Hamer et al. 1985).

During 1976–77, searches were made in a core area of approximately 150 km². During 1978–80, however, the radio-collared bears directed much of our field activity, and because of the bears' movements we worked within a larger study area of approximately 250 km². In the 1st 2 years, searches were made on essentially linear travel routes ("transects"). In the last 3 years, many of our searches were directed by radio-tracking; in these cases, the quality of the radiolocation usually determined the size of the area to be searched. Inaccurate radiolocations covering an area of 0.5 km² or larger generally were not searched. Food and habitat use was recorded only after direct observations of foraging bears or discovery of feeding signs. Information was not inferred by superimposing radiolocations on habitat cover maps.

Feces were analyzed by removing 5 (285 feces) or 10 (120 feces) 10-ml subsamples and examining these, in 5-ml portions, under 7–40 power magnification. Items were identified and assigned by visual estimate to 1 of 8 percentage volume classes. Two estimates of volume then were calculated: the minimum volume for the item, calculated using the lower values of the

8 volume classes; and the maximum volume, calculated using the upper values of the volume classes. The mean values so determined then were used in a similar manner to calculate mean minimum and mean maximum values for each semimonthly period. These manipulations depart from the common method of using the midpoint of each volume class to obtain a single estimate of volume. It is invalid to convert ordinal data to ratio data (Hinkle et al. 1979:47). These laboratory methods were not applied to 13 feces of simple composition that were analyzed in the field.

Vegetative items collected for chemical analysis were air-dried at room temperature. Each sample consisted of several hundred individuals when small plants, such as horsetails, were collected. When roots or the aerial portions of large plants such as cow parsnip (*Heracleum lanatum*) were collected, the sample was made from several tens of individuals. Each sample was collected from 1 site of a few tens of square meters. Crude protein was determined by standard proximate analysis (Kjeldahl method). Fiber was determined by acid detergent analysis (AOAC 1980).

Annual variation in buffaloberry fruit production was estimated in permanent transects. Transects were run on contour, with plots at 50- or 100-m intervals. At each plot, all fruits were counted that occurred within 4 m of a permanent marker tree.

For habitat analysis, the following terms and procedures were used. "Feeding records" are the values determined by combining minutes of feeding (recorded during direct observations of bears) with numbers of feeding signs (recorded during ground searches). When both minutes of feeding and number of feeding signs were available for a feeding event, only 1 of these data sets was used to prevent duplication. "Feeding sites" were defined as contiguous feeding areas with the same environmental parameters. "Major feeding sites" were defined by eliminating the least important sites from the data base. This was done by ranking the feeding sites by amount of use and then excluding 10% of the sites at the low-use end of the rank order. Statistical analyses were applied to the "major sites" to reduce the skew that minor sites could have caused (e.g., sites containing only 2 or 3 diggings). Each remaining, or "major," feeding site then was weighted equally in statistical tests. Sites, rather than feeding records, were used for statistical tests because feeding records were not independent: once a site was discovered, all or most

feeding activity likely was recorded for the immediate area. However, feeding records were used in Table 2 because they accurately incorporated site importance by accounting for the amount of feeding at each site.

FOOD HABITS, PLANT PHENOLOGY, AND CHEMICAL COMPOSITION

Figure 2 and Table 2 present the results of fecal analysis and the compilation of feeding records, respectively. *Hedysarum* roots were eaten primarily early and late in the year, before and after green forage or fruits were most available. The roots' nutritive content appeared to be high at these times as well (Figs. 3 and 4).

Use of *hedysarum* roots declined as the spring growing season progressed (Fig. 2, Table 2), which may have been related in part to a decline in the roots' nutritive value (Figs. 3 and 4). Seasonal changes in root quality were investigated in detail at 4 sites by collecting pink *hedysarum* roots at different phenological stages. The data indicated significant seasonal changes (Friedman 2-way analysis of variance by ranks for nonnormal data, $df = 4$, $P < 0.01$ [protein], $P < 0.02$ [fiber]). Sampling of yellow *hedysarum* was insufficient for statistical analysis; however, the similarity between Figures 3 and 4 suggests that comparable changes may have taken place in both species.

We recorded little use of *hedysarum* roots by grizzly bears when *hedysarum* was in flower (Table 3). Crude protein of pink *hedysarum* roots was at its lowest point during flowering. Considering the samples from our 4 sites, a significant difference in crude protein content was found between roots from preleaf plants and roots from flowering plants (Friedman multiple comparison technique, $P < 0.05$; Daniel 1978:231). Roots from flowering plants also had significantly higher fiber content ($P < 0.10$). Although the declining use of roots during June may have been related partly to a decline in their nutritive value, the increasing availability of green forage also must have been important.

During late July and early August, *hedysarum* roots again entered the diet in 3 of 4 years (Fig. 2). *Hedysarum* was in late flower and early seed at that time. Although the nutritive value of the roots seemed to increase as the plants entered the seeding stage (Figs. 3 and 4), neither the increase in protein nor the decrease in fiber was statistically significant according to our 4 paired samples of pink *hedysarum*

Table 1. Major subalpine vegetation types in the study area (see also Holland and Coen 1983, Hamer 1985).

Vegetation type	Scientific names	Characteristics
1. Spruce or pine/grouseberry forest	<i>Picea glauca</i> × <i>P. engelmannii</i> or <i>Pinus contorta/Vaccinium scoparium</i>	Upper subalpine forest, typically on north- through east-facing aspects. Spruce regeneration usually found in the understory of the pine variant.
2. Spruce or pine/buffaloberry forest	<i>P. glauca</i> × <i>P. engelmannii</i> or <i>P. contorta/Shepherdia canadensis</i>	Often southeast-southwest aspects. Spruce variant occurs on moister sites or more northerly aspects.
3. Spruce/willow open forest	<i>P. glauca</i> × <i>P. engelmannii/Salix glauca</i>	Regeneration from the 1936 fire, on moderate slopes with north- through east-facing aspects. Scattered, immature spruce over willow and buffaloberry. Scattered groves or individuals of spruce over a dense shrub layer of type 7A.
3A. Upland open forest		
3B. Valley bottom open forest		
4. Spruce-subalpine fir/feathermoss forest	<i>P. glauca</i> × <i>P. engelmannii-Abies lasiocarpa/Hylocomium splendens</i>	Moist, often north- through east-facing slopes.
5. Spruce-horsetail forest	<i>P. glauca</i> × <i>P. engelmannii/Equisetum arvense</i>	Typically streamside or on other sites with a high water table (e.g., terraces, seepage sites). Tall, streamside willows occur in a few sites.
6. Spruce/laborador tea-crowberry/peatmoss open forest	<i>P. glauca</i> × <i>P. engelmannii/Ledum groenlandicum-Empetrum nigrum/Sphagnum</i> spp.	On gentle, east-facing slopes with impeded drainage and standing water between hummocks.
7. Willow shrubfields	<i>S. glauca, S. ferrae-Betula glandulosa/Elymus innovatus</i>	Widespread and very variable in the study area. On terraces, valley bottoms, moderate, lower slopes with seasonally high water table. Lower subalpine. Dense shrubfields on steep east-facing slopes that would succeed to spruce forest without recurring avalanches. A subhygric variant of type 7A in sites with a higher water table such as seepage sites and pond-sides. Upper subalpine and lower alpine shrubfields in wet meadows, on streambanks, and so forth.
7A. Willow-dwarf birch/hairy wild rye shrubfield		
7B. Willow-dwarf birch avalanche shrub		
7C. Willow/horsetail shrubfield		
7D. Barratt's willow shrubfield		
7E. Rock willow shrubfield	<i>S. vestita</i>	In the timberline zone on steep, north-facing slopes with seepage and snow accumulation.
8. Buffaloberry/hairy wild rye shrubfield	<i>S. canadensis/E. innovatus</i>	Moderate to steep southeast- through west-facing slopes where xeric conditions have inhibited the regeneration of lodgepole pine after fire.
9. Hairy wild rye-brome-rough fescue (RBF) meadows	<i>E. innovatus-Bromus pumpellianus-Festuca scabrella</i>	On steep, usually exposed southeast-through west-facing slopes with deep soils. Forest regeneration is inhibited by a complex of factors: wildfire; intense solar radiation; chinook winds; xeric, well-drained, often colluvial soil; avalanching in some sites; and perhaps grazing.
9A. RBF meadow		
9B. Junegrass-brome-sage meadow		
9C. Bearberry/RBF/dwarf shrub meadow	<i>Arctostaphylos uva-ursi</i>	An edaphic and grazing variant of type 9A. On steep south-facing slopes where soil is stony, shallow, and often terraced. On steep, south- through west-facing slopes where bearberry and often colluvium have high coverage.

Table 1. Major subalpine vegetation types in the study area (see also Holland and Coen 1983, Hamer 1985). (Continued)

Vegetation type	Scientific names	Characteristics
9D. Larkspur-wheatgrass-RBF meadow	<i>Delphinium glaucum</i> - <i>Agropyron</i> spp.	Mesic variant of type 9A, usually in shallow gullies and zones of slight snow accumulation. Tall herbs occur.
9E. Horsetail-RBF meadow	<i>E. arvense</i>	Localized seepage areas in the type 9A zone, where tall herbs and horsetail are abundant.
9F. Mountain timothy-wheatgrass-woodrush-sedge meadow	<i>Phleum alpinum</i> - <i>Agropyron</i> spp.- <i>Luzula parviflora</i> - <i>Carex</i> spp.	Upper subalpine meadow, often in openings at timberline on deep soil where snow accumulates.
9G. Cow parsnip tall herb meadow	<i>Heracleum lanatum</i>	Tall herb community in the upper subalpine, in seepage, or along intermittent streams.
10. Wet meadows	<i>E. arvense</i> , <i>Oxyria digyna</i> , <i>Senecio triangularis</i>	Various wet meadow and streamside types with high coverage of herbs, including types with high coverage of horsetails, mountain sorrel (<i>Oxyria digyna</i>), and ragwort (<i>Senecio triangularis</i>). Usually near timberline.
11. Alpine types		Heaths, heathers, dwarf willow, dry graminoid meadows, and so forth, that were unimportant as grizzly bear feeding habitat and are not described here.

roots (Friedman multiple comparison procedure, $P > 0.25$). A larger sample size may have shown a significant difference for fiber; compare the widely separated values of the samples in Figure 3.

Horsetails (*E. arvense*) were the main food of grizzly bears during early summer (Fig. 2). We found no evidence during examination of numerous feeding sites that a similar species, *E. pratense*, was eaten. As horsetails matured during July and early August, use of this food declined. This result is expected because as herbs mature, digestible energy and protein decline and structural elements such as cellulose and lignin increase (e.g., Klein 1965). Our results suggested a similar decline in the crude protein content of horsetails (Fig. 5). When bears fed on roots in late July or early August, they may have been responding to this decline in horsetail quality, to an increase in hedysarum root quality, or both.

Graminoids (grasses, sedges, and rushes) were another major component of the grizzly bears' green forage from May through September (Fig. 2). According to microhistological examination of fecal samples for 1976 (Hamer 1977), most graminoids were grasses; sedges and rushes were of minor importance. Cow parsnip and mountain sorrel (*Oxyria digynia*) also were common forage items. Mountain sorrel may be underrepresented in feces (Russell et al. 1979:73). It is high in crude protein (23%–29%,

$N = 3$) and low in fiber (15%–21% acid detergent fiber [ADF]) in early phenological stages. Cow parsnip leaves also have high crude protein content (22%–31%), but it is the stem and petioles that usually are eaten. In fact, discarded leaves at the base of a cropped cow parsnip plant indicate grizzly bear feeding activity. Stems and petioles are relatively high in fiber (35%–50% ADF) and low in crude protein (7%–11%). Blossoms of cow parsnip are also eaten, although this was observed rarely in our study area.

The intensity and duration of buffaloberry feeding was positively associated with our fruit production index, although these trends were not established statistically (Table 4, Fig. 6). In years of lower fruit production, hedysarum roots constituted a greater volume of the August–October fecal samples. This also was observed in Jasper National Park (Russell et al. 1979) and in the Yukon (Pearson 1975). Other, less abundant fruits in the study area were secondary in the bears' diet. We recorded consistent use of low-bush blueberries (*Vaccinium myrtillos*) and grouseberries (*V. scoparium*) by 1 of our radio-collared bears from 1977 to 1979. Sugar content of fruits was not determined; however, Craighead and Sumner (1982:70) reported values of 34% and 40% sugar content for buffaloberry and grouseberry, respectively.

Ants (Formicidae) occurred frequently in the

Table 2 Grizzly bear food habits during 1976–79 as indicated by observations of foraging bears and examination of feeding sites.^a

	Early May	Late May	Early Jun	Late Jun	Early Jul	Late Jul	Early Aug	Late Aug	Early Sep	Late Sep	Early Oct	Late Oct	Early Nov
Roots													
Pink hedsarum	655	1,170	567	1,162	29	1,019	455	38	125	—	1,093	306	56
Yellow hedsarum	1,598	1,914	574	84	—	—	77	24	183	3	1	1,050	399
Herbs													
Horsetail	—	—	10	221	1,477	1,374	105	10	—	—	—	—	—
Mountain sorel	—	—	—	32	42	25	—	—	8	—	—	—	—
Cow parsnip ^b	—	—	—	14	185	143	—	—	14	—	—	—	—
General grazing ^c	333	100	68	46	26	25	—	—	—	—	—	—	—
Fruits													
Buffaloberry	—	—	—	—	—	—	242	1,042	790	600	404	719	90
<i>Vaccinium</i> spp.	—	—	—	—	—	—	—	—	155	—	—	92	—
Bearberry	574	110	12	100	—	—	—	—	—	—	—	192	66
Ants^d													
In or under deadwood	—	—	—	25	184	304	83	16	19	1	—	—	—
In ground nests	28	—	—	16	73	31	64	7	—	—	—	—	—

^a Minutes of feeding (M) and numbers of signs (S) were combined into "feeding records" by converting S to M. Conversion factors were estimated, when possible, by analyzing sites where both M and S were known. The following approximations were used: hedsarum, 1.4 min/digging signs where time of use was also known; cow parsnip, 0.9 min/cropping (63 signs); other herbs, 0.1 min/cropping (rough estimate); buffaloberry, 3.0 min/sign (80 signs); *Vaccinium* and bearberry, all data from direct observation; ant feeding signs, 1.0 min/sign (rough estimate). The errors that may be generated by applying these estimates are believed slight compared to the biases resulting from the differing degrees of conspicuousness of various field signs. Within these limitations, useful comparisons can be made, particularly within rows. Field effort was relatively constant from May through October of each year. Moreover, because the values in this table are the sum of 4 years of observations, the effect of year-to-year variation in field effort during semimonthly periods should be further reduced. However, because field effort was not controlled, only major differences within rows (e.g., order of magnitude differences) should be considered significant.

^b The early September record consisted of 11 min of feeding on inflorescences and 3 min on stems and petioles. All other records were of stems, petioles and, occasionally, leaves.

^c According to fecal analysis and plant community analysis, at least 90% of this general grazing activity represented grazing on grasses, sedges, and rushes.

^d Ants included *Camponotus herculeanus*, *Formica dakotensis*, and *F. neorufibarbis* (Andre Francoeur, pers. commun.). Of records of ants in ground nests, 96% were of ants under flat stones, and 4% were of ants in thatch-mound nests made of ground litter not associated with deadwood.

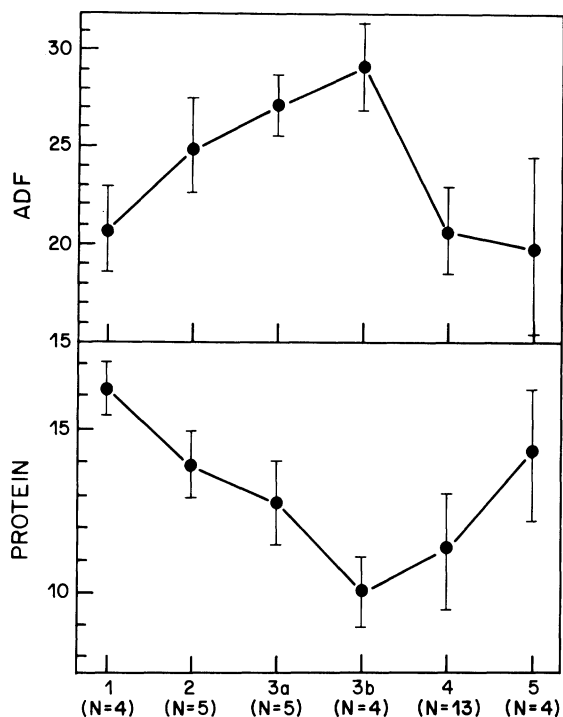


Fig. 3. Percent crude protein and acid detergent fiber (ADF) of pink hedysarum roots collected in the study area. Vertical lines indicate 1 SD above and below the mean. 1 = preleaf; 2 = leaf; 3a = flowers budding; 3b = flower; 4 = seed; 5 = cured.

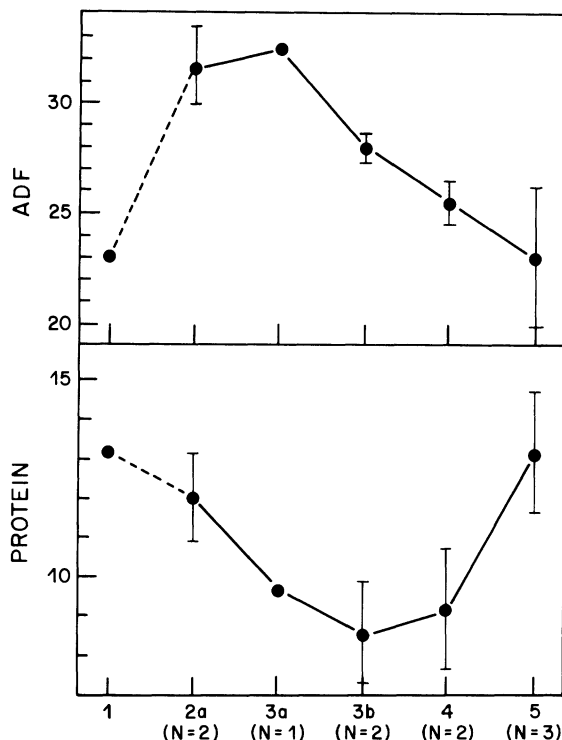


Fig. 4. Percent crude protein and acid detergent fiber (ADF) of yellow hedysarum roots. See Figure 3 for details. Values for stage 1 (preleaf) are represented using values from stage 5 (cured).

bears' diet. Of the 329 feces analyzed from early May to early September, 161 (49%) contained ants. As Eagle and Pelton (1983:98) point out, "As a monogastric species...bears have a requirement for certain amino acids, and even a small quantity of animal material in the diet may meet this requirement."

Mammals were eaten by grizzly bears when opportunities arose. Elk (*Cervus elaphus*) calves were hunted in late May and early June (Hamer and Herero, unpubl. data). Grizzly bears scavenged and possibly killed adult male elk during the elk's September mating season. Minor use of ground squirrels (*Spermophilus columbianus*) was recorded; only 46 fresh

diggings were noted during 1976-79. Fish apparently were not eaten by grizzly bears in the study area.

HABITAT USE

Table 1 summarizes vegetation types where grizzly bears foraged. Pink hedysarum roots were dug almost entirely in mesic to subhygric willow shrubfields (vegetation type 7A). Certain site parameters were associated with this habitat: 97% of the classified records occurred below 2,000 m, and 83% were on slopes less than 25°.

Yellow hedysarum roots generally were dug in

Table 3. Use of hedysarum roots by grizzly bears in relation to phenology.*

	Phenological stage				
	Pre-emergence	Leaf	Flowers budding or open ^b	Seed	Cured
Pink hedysarum	1,358 (18)	2,220 (30)	858 (12)	1,471 (20)	1,455 (20)
Yellow hedysarum	3,267 (55)	937 (16)	48 (1)	274 (5)	1,467 (24)

* Feeding records were calculated as described in Table 2. Values in parentheses are percentages.

^b Hedysarum in flower often was at a late flowering stage. For example, 59% of the pink hedysarum records (N = 360) were from sites where the phenology of dug plants was partly late flower and partly early seed.

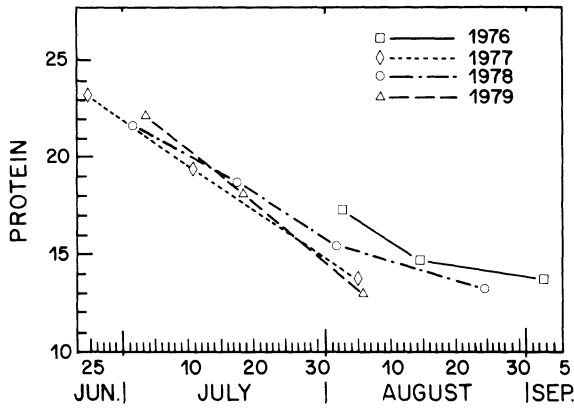


Fig. 5. Percent crude protein of horsetail (aerial portions) collected from the "16 mile" site. Values are single data points from single samples.

drier habitat, usually in mesic to xeric, steep meadow slopes (e.g., types 9A, C, D). Over 90% of the dry meadow sites occurred above 1,900 m on slopes steeper than 24°; 66% percent of the classified records faced southeast-west (135°-269°). In addition, 7% of the classified yellow hedysarum diggings occurred in subhygric, upper subalpine shrub types, notably in rock willow vegetation (type 7E).

Horsetails were eaten in mesic to hygric habitat, where soil moisture was high at least seasonally. Locations included streambanks, gully bottoms, sidehill seeps or springs, and areas of impeded drainage such as fens or other wet meadows. Horsetail feeding occurred from valley bottom to the upper limit of the subalpine zone at about 2,300 m. Of our classified feeding records, 79% occurred on slopes less than 15°. Feeding records occurred at various aspects; soil moisture and other microhabitat conditions seemed more important than slope aspect. North-facing records were only slightly more common than south-facing (56% vs. 44%). A similar relationship was found when horsetail feeding sites were analyzed: 40 of the 66 major sites faced north and 25 faced south ($X^2 = 3.0$, $df = 1$, $P > 0.05$).

The majority of the horsetail feeding records (61%) were found in a band 1 m to tens-of-meters wide along streams. The U shape of both large valleys and certain small tributaries apparently was instrumental in providing suitable site conditions. Some small tributaries, for example, were literally U-shaped, with steep banks on each side of the stream leading down to a flat bed, 1 to a few meters wide, of which the stream occupied only a small portion. In the flat bed, horsetail cover often exceeded 75%.

Information on graminoid feeding habitat was limited because of observational bias. Unlike horsetail feeding signs, graminoid feeding signs were difficult to discern and, moreover, could not be distinguished readily from signs left by ungulates. Direct observations of foraging bears revealed considerable grazing on graminoids in the dry meadows also dug for yellow hedysarum roots (Table 1). However, grazing in other, less open habitat likely occurred, but rarely were we able to identify specific feeding sites.

Grizzly bears ate buffaloberries in sites where the cover of buffaloberry shrubs varied from dense (cover >75%) to scattered (<5%). In some sites, willow and dwarf birch dominated the shrubfield. The relative use of each vegetation type could not be determined accurately because feeding signs became less conspicuous late in the season as leaves began to fall, and because we obviously could see bears in shrubfields more easily than in forest. Because of these biases, our results suggested but could not quantify that bears used 2 subhygric to mesic willow-dominated vegetation types, 3A and 7B, to about the same

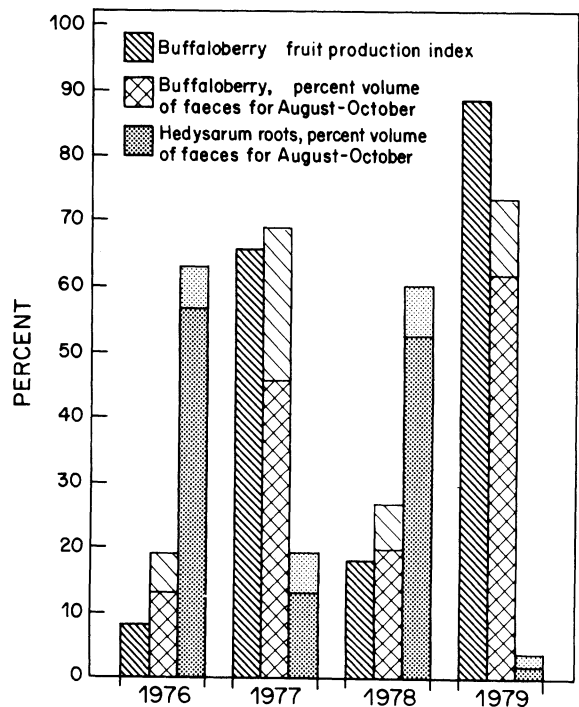


Fig. 6. Buffaloberry fruit production index compared with grizzly bear use of buffaloberry fruits and hedysarum roots during August-October, 1976-79. Grizzly bear use was determined from percentage volume of foods in fecal samples; the range between minimum and maximum estimates of volume is shown by lighter shading.

Table 4. Buffaloberry fruit production at 3 transect areas in Banff National Park.**Table 4a.** Relative indices of estimated annual fruit production, 1976–80. Indices are reported relative to 100, which was assigned arbitrarily to the largest count (after correcting for differing areas sampled at each transect).

Transects	N	1976	1977	1978	1979	1980
Low-elevation (1,400 m) ^a	25	—	3	0.4	15	—
Mid-elevation (1,700 m)	21 ^b	10–15 ^c	32	10	96	31
High-elevation (2,100 m)	11	2–7 ^c	99.9	27	80	100

^a The low-elevation transect was in the main Bow Valley, 20 km southwest of the study area.^b In 1979, 9 stations were counted, a subsample as a result of the abundance of fruit. In 1980, only 4 stations were counted because of time constraints.^c Estimate based on general field notes made in 1976 in the transect areas.**Table 4b.** Analysis of buffaloberry transect data for 1977–79 using the Friedman 2-way analysis of variance by ranks and corresponding multiple comparison procedure.^{a,b}

Low-elevation transect

FTS = 35.5, df = 2, $P < 0.001$

1979 > 1977 > 1978

*** **

Mid-elevation transect

FTS = 18, df = 2, $P < 0.001$

1979 > 1977 > 1978 > 1976

* * (est)

High-elevation transect

FTS = 17.6, df = 2, $P < 0.001$

1977 > 1979 > 1978 > 1976

NS *** (est)

^a Daniel 1978:224, 231.^b FTS = Friedman test statistic; NS = no significant difference between years; * = significant difference, $P < 0.10$; ** = $P < 0.05$; *** = $P < 0.01$ (experiment-wise error rates); est = estimate (see Table 4a). Note: 0.10 level of significance considered appropriate for multiple comparison tests; see Daniel 1978.)

degree as the mesic to subxeric buffaloberry/hairy wild rye types 2 and 8 (Table 1).

Low-bush blueberries and grouseberries were eaten in open stands in the spruce-subalpine fir-larch (*Larix lyallii*)/grouseberry forest. Both *Vaccinium* species were important fruit-producing shrubs, but compared to buffaloberry, their total production appeared to be minor in our study area. The feeding sites were located in the southwest corner of the study area on east-facing slopes at and above 2,000 m. Tree cover was 25% or less. Our observations in these open forests may have been biased: we obviously could not see bears in heavily forested habitat, and we could not record *Vaccinium* feeding without seeing bears directly because *Vaccinium* feeding signs are very inconspicuous. However, we did not observe comparable *Vaccinium* fruit production anywhere else in the study area during the 1976–79 period, suggesting that our data for *Vaccinium* feeding habitat may have been indicative of grizzly bear use. The common occurrence of *Vaccinium*-containing feces in this spe-

cific habitat and their apparent absence in other grouseberry forests of the study area also supported this contention.

Bears fed on bearberries and ants under stones in many of the same dry meadows that they fed in for yellow hedysarum roots and graminoids. Seventy-seven percent of the bearberry feeding records were on slopes facing south-southwest (180°–224°), reflecting an occurrence on very exposed, often xeric, slopes.

SEASONAL CHANGES IN HABITAT USE

Pink Hedysarum

Digging sites for pink hedysarum were at lower elevations in May than in June (records for early July were negligible; see Table 2). The 28 classified major digging sites in May had significantly lower elevations than the 15 major sites for June (Mann-Whitney U test for nonnormal data, 32.5, 387.5; $P < 0.001$). Bears may have dug for pink hedysarum at higher elevations as the spring progressed because hedysa-

rum roots had higher nutritional value in earlier phenological stages and, other site conditions being equal, higher-elevation sites develop later in the spring.

If grizzly bears dig in later-developing sites to feed on roots of earlier phenological stages, then they also might be expected to feed more on north-facing slopes and less on south-facing slopes as the seasons progress. Our observations supported this supposition, according to the distribution of the 37 classified major sites for pink *hedysarum* by month (May vs. Jun) and aspect (north vs. south) ($X^2 = 8.1$, $df = 1$, $P < 0.01$).

Although these seasonal changes support the hypothesis that during June grizzly bears dug pink *hedysarum* in sites where phenology was retarded, it also could be postulated that bears simply dug in sites that were available. As sites thawed or became snow-free, for instance, bears could dig in these or any other available sites. If this were the case, however, then June diggings would be expected in early- and late-developing sites. The data on slope aspect do not support this: in late June, for example, only 1 of 8 sites faced south, suggesting that retarded phenology was important.

Yellow *Hedysarum*

Because exposed, dry meadows were free of snow early in the spring at essentially all elevations, we did not expect an increase in the mean elevation of yellow *hedysarum* digging sites as the spring progressed. It was, however, observed. The mean elevation of the 28 major early May sites was $2,024 \pm 111$ m (mean ± 1 SD), a figure significantly lower than the mean for the 31 late May and June sites, $2,138 \pm 99$ m ($t = 3.75$, $df = 47$, $P < 0.001$: data fit the assumptions of normality and homogeneity of variance). The late May and June sites were combined because their means were not significantly different. The 6 early and 2 late June sites could not be separated because of small sample size; according to our observations, yellow *hedysarum* was a minor food in late June (Table 2).

The observed seasonal increase in elevation was not caused by grizzly bears' use of high-elevation mating areas (cf. Herrero and Hamer 1977) or high-elevation rock willow shrubfields (type 7E). A significant difference remained when these 6 sites were deleted ($P < 0.02$). Possibly the increase was related to a somewhat slower phenological development at

higher elevations caused by the temperature decrease that occurs with increasing elevation (lapse rate, approximately 5 C/1,000 m). Differential availability of other dry meadow foods such as bearberries, graminoids, and ants under stones also could have influenced grizzly bear habitat choice for these and yellow *hedysarum* feeding sites.

Use of rock willow shrubfields (type 7E) later in the spring influenced the slope aspect of June data. Of classified major sites, 78% ($N = 40$) were on south-facing slopes in May compared to 29% ($N = 7$) in June ($X^2 = 6.8$, $df = 1$, $P < 0.01$). There was no significant difference between early and late May in the distribution of north- vs. south-facing sites. By using the upper elevation, northeast-facing rock willow sites in June, grizzly bears could continue to dig yellow *hedysarum* in early phenological stages. Some yellow *hedysarum* plants dug in late June on northeast-facing, upper-elevation slopes, for example, were still in the preleaf stage.

Horsetails

A significant difference was found in the elevational distribution of the 8 June, 30 early July, and 28 late July–August classified major sites (Kruskal-Wallis analysis of variance for nonnormal data, $H = 24.5$, $df = 2$, $P < 0.001$). The sites were classified in this way because there were only 2 August sites (1 Aug 1979). The elevations of the late July–August sites were significantly higher than those from early July (multiple comparison procedure, $P < 0.05$; Daniel 1978:213). The use of higher-elevation sites later in the season evidently was 1 way grizzly bears continued to find emerging or at least relatively immature horsetails with their higher nutritive value.

No notable differences in slope aspect of horsetail feeding sites were found as the summer progressed. We already have noted that there were only slightly more feedings on north- vs. south-facing slopes for the whole season combined. Grizzly bears' selection of horsetail feeding sites seemed to involve the use of very specific microhabitat (e.g., streamsides, gully bottoms) at successively higher elevations, with slope aspect apparently a minor factor.

Buffaloberry

We did not record a tendency for grizzly bears to begin feeding on buffaloberries in low-elevation sites, where one might expect the 1st-ripening fruits to be found. There was no significant difference in the dis-

tribution of elevations for the 7 early August, 13 late August, and 13 early September classified major sites (Kruskal-Wallis analysis of variance for nonnormal data, $P > 0.30$). The effect of elevation evidently was overshadowed by other factors such as aspect and forest coverage—given the narrow elevational band of buffaloberry habitat in our study area (approximately 1,600–2,100 m), and given the fact that the lower-elevation sites were forested (type 2) and therefore less exposed to sunlight. Grizzly bears with larger home ranges may have descended to lower elevations. For example, some bears may have descended to the montane zone, about 15 km south of our study area in the main Bow Valley.

Nor was a clear seasonal change recorded for slope aspect of buffaloberry feeding sites. Of the classified major sites, 71% ($N = 7$) from early August were south-facing, compared to 38% ($N = 13$) from late August, but the difference was not significant ($X^2 = 2.0$, $df = 1$, $P < 0.20$). The 13 early September sites had the same distribution as those for late August, with 38% south-facing. Thus, there seemed to be a tendency for grizzly bears to feed on south-facing slopes early in the buffaloberry season, where the 1st ripe fruits presumably would have been found, but this tendency was not statistically significant, perhaps partly because of our small sample size for early August.

WILDFIRE AND HABITAT USE

Important feeding habitat for grizzly bears in our study area often was fire successional. This included, for example, some pink and yellow *hedysarum* digging habitat in willow-dwarf birch and dry meadows, respectively, and most if not all buffaloberry and *Vaccinium* feeding habitat. Wildfire's influence on grizzly bear feeding ecology in our study area is the subject of a companion article (Hamer and Herrero, this volume).

BIASES AND VALIDITY OF RESULTS

Because only 2 grizzly bears were radio-tracked during our study, our results emphasized these 2 animals. The question remains as to whether our results accurately reflected the feeding ecology of grizzly bears in our study area. We addressed this question 1st by comparing fecal analysis data obtained without the aid of radio-tracking (1976–77) to data obtained when the 2 females were radio-tracked (1978–79). (We estimated that 50%–60% of

the feces collected from 1978 to 1979 were from radio-collared animals.) For this comparison, minimum indices of similarity (cf. Mueller-Dombois and Ellenberg 1974:220) were calculated for each of the 12 semimonthly periods (Hamer 1985:177–188). A relatively close convergence of the 2 data sets was indicated; the minimum indices of similarity for the 12 semimonthly periods totaled 810, with 10 of the 12 indices exceeding 60. In contrast, much lower indices of similarity were obtained when we compared the 2 years when radio-tracking was not used, 1976 and 1977. For these 2 years, the minimum indices totaled 580, with only 4 of the 12 indices exceeding 60. In the same manner, a comparison between the 2 years when radio-tracking was used, 1978 and 1979, gave a total of 577, again with only 4 indices exceeding 60. These results show that the indices of similarity obtained when data from 1976 to 1977 and 1978 to 1979 were compared actually are higher than might be expected. Evidently we did not bias our food habits data in any obvious way when we concentrated our field effort on the radio-collared bears. Although the radio-collared bears undoubtedly showed some individual variation in food choice, this influence could not be discerned given the greater variation from other sources such as sampling error and annual variations in food availability. (For instance, the low indices obtained above, 580 and 577, stem largely from annual differences in availability of buffaloberry fruits. Buffaloberry fruits were more abundant in feces in 1977 and 1979 than in 1976 and 1978; see Fig. 2. Therefore, when data from 1976–77 are compared with data from 1978–79, years of high and low buffaloberry abundance are combined and “cancel each other out,” giving the higher degree of similarity.)

We made a similar comparison to assess the validity of our habitat use data. Reasonable convergence again was shown between data obtained from the radio-collared bears and from unmarked bears (Hamer 1985). Exceptions were horsetail (index of similarity 60) and buffaloberry (index 46; absolute equality would give an index of 100). More horsetail feeding records from radio-collared bears were in spruce/horsetail forests (type 5; 46% vs. 15% for unmarked bears). This probably represents, in part, a bias against discovering feeding signs in mature spruce forest without the aid of radio-tracking. Conversely, the high percentage of feeding records from unmarked bears in open wet meadows (type 10) likely resulted, in part, from the bias toward seeing bears

in open habitat (56% vs. 31% for radio-collared bears). With regard to buffaloberry, the feeding records from unmarked bears were weighted toward types 2 and 8 (74% vs. 20% for radio-collared bears). Records from the radio-collared bears were more often in types 3 and 7B (74% vs. 25% for unmarked bears). Buffaloberry feeding signs were difficult to recognize in some circumstances, and this probably led to errors in assessing use. We can only speculate how much of the difference between the 2 data sets was caused by differences in habitat preference between the radio-collared bears and other bears in the study area.

In general, however, we believe that our methods, although subject to their own biases, provided reasonably accurate, convergent samples of the feeding ecology of grizzly bears in our study area. We attributed the consistency of results in large part to the simplicity of the Front Range ecosystem—simple in the sense that we did not identify any notably different feeding opportunities in or near the study area that could have been exploited by other, differently behaving grizzly bears. Also relevant is that our food habits results are similar to those from Jasper National Park, an ecologically similar area 200 km north (Russell et al. 1979).

DISCUSSION

The grizzly bear can be compared to horses and other perissodactyls (Mealey 1980), which, lacking a rumen, tend to pass food through their digestive systems more quickly than ruminants, extracting fewer nutrients from the same forage but compensating by their higher rate of passage (Janis 1976). The grizzly bear, with its simple digestive system, takes this strategy further than the horse, eliminating cecal fermentation and extracting only the most digestible components of food.

It is apparent, then, why grizzly bears generally feed most on green vegetation in the spring and early summer. At this time, leaves and stems are immature and thus high in soluble nutrients and low in structural cellulose and lignin. For instance, Sizemore (1980:33) found that grizzly bears in his study area did not select specific plant parts when grazing early in the growing season, but once the plants had flowered, bears selected blossoms rather than leaves and stems. Blossoms had a digestible (soluble) nutrient content similar to the preflowering herbage. Atwell et al. (1980) found that sedge (*Carex macrochaeta*)

made up about 97% of the Kodiak brown bear's diet for 5 or 6 weeks, at which point the bears abruptly left to fish for salmon at lower elevations. Although the bears left these sedge communities when spawning salmon were available, this switch also corresponded with the end of new sedge growth: by mid-August, melting snow began to expose high-elevation ash and scree rather than sedge communities. Moreover, the bears departed earlier in 1974—a year when snow melt was about 2 weeks earlier than in the other 2 years of the study. Plant phenology therefore seemed as important in determining the duration of sedge feeding as the return of spawning salmon. Our observations during the green vegetation feeding period showed a similar definition, with horsetail feeding usually tapering off rapidly during early August.

Despite this, grazing often is recorded late into the autumn. In Mealey's (1980) study area, bears continued to graze into the post-growing season by selecting moist sites such as stream bottoms, springs, and snowbed communities. Succulent grasses may remain physiologically active late into the autumn and have been shown to have significantly higher protein content than drier grasses from exposed, adjacent grassland locations (Graham 1978).

The grizzly bear's need for foods high in digestible solubles and low in fiber explains why green plants normally are eaten in their immature stages, and it also explains why certain seasonal movements occur. We recorded higher elevations of horsetail feeding sites as the season progressed from mid-June through early August. By July, plants at lower elevations were relatively mature, showing reduced protein levels. Recently emerged plants at higher elevations, however, had higher protein levels comparable to those that had been found in lower-elevation horsetails several weeks earlier (Hamer 1985). Higher-elevation sites thus had the advantage of retarded phenology, but absolute protein levels also may have been higher. Johnston et al. (1968) found that alpine tundra grasses contained about 50% more crude protein than grass from the fescue (*Festuca* spp.) prairie at the same phenological stage. A similar relationship may hold for horsetail from upper vs. lower subalpine sites.

Stelmock (1981:59) similarly recorded horsetail grazing about 2 weeks later in his higher-elevation study area, and he observed this same pattern for grass grazing. Mealey (1980:285) found that grizzly bears feeding on grasses, sedges, and spring beauty in his Yellowstone study area "began in snow-free

locations and followed snowmelt and green-up to the highest elevations by late June.”

Presumably because of the specialized microhabitat where horsetails grew, we did not record differences in slope aspect of horsetail feeding sites as the summer progressed. A switch to north- and east-facing slopes otherwise is expected if grizzly bears are searching for sites where plant phenology is retarded. Martinka (1972) suggested that grizzly bears feeding on cow parsnip in Glacier National Park, Mont., used these aspects as snow melted during the summer. We did record the predicted switch to more northerly aspects, as well as an increase in the elevation of feeding sites, as the hedsarum root digging season progressed from early May through late June. Hedsarum roots, in this early part of the growing season, showed the same trends in nutritive content as did green vegetation, namely a decrease in crude protein and an increase in fiber. It appeared that grizzly bears dug hedsarum roots in later-developing sites during June to find plants of earlier phenological states and, therefore, of higher nutritive value.

Mundy and Flook (1973) believed that grizzly bears in the Canadian national parks moved from the subalpine zone in the spring, up to the alpine zone in the summer, and back down to lower elevations in the autumn. Martinka (1972) recorded a similar pattern for at least a portion of the grizzly bears in Glacier National Park, Mont., with bears frequenting low elevations in the spring; higher-elevation forest and alpine areas in the summer and early autumn; and lower-elevation forests in late autumn. This pattern was confirmed for the nearby Mission Mountains population using radio-collared grizzly bears (Servheen 1981).

This description did not apply to the grizzly bears in our Banff study area. Early season feeding occurred at relatively high elevations in dry, steep meadows where yellow hedsarum roots, bearberries, graminoids, and ants under stones were eaten. Most of this feeding was above 1,900 m. These dry meadows—with their southeast-southwest aspects, steep slopes, and exposure to chinook winds—were snow-free very early in the spring. Later in the spring, grizzly bears still could be found in these dry meadows (often on more northerly aspects) or in valley bottom locations. At these lower elevations, bears fed on pink hedsarum roots and, by June, emerging horsetails. A similar pattern occurred in autumn, when bears used pink and yellow hedsarum roots in their respective habitats. During midsummer, subalpine elevations

were used. The alpine vegetation of our study area, however, was unimportant as grizzly bear feeding habitat.

It appears that through a combination of food and habitat selection, the grizzly bear eats plant foods high in soluble nutrients and relatively low in fiber. As the growing season progresses, for example, bears often choose feeding sites of earlier phenology by moving to higher elevations or onto shaded, north-facing slopes. This largely herbivorous carnivore supplements its diet with animal foods when they are available. Even a food comprising less than a few percent of the diet, such as ants, may provide essential amino acids (Eagle and Pelton 1983). In our study area, the late summer fruit crop provides bears with an often superabundant source of easily digested sugar during the predenning “hyperphagic” period (Nelson et al. 1983). In these ways, the world’s 2nd largest carnivore can assume a diet that often is more than 90% vegetative matter.

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