The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia

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Abstract: Based on the analysis of 1100 feces or scats, the seasonal diet of grizzly bears (*Ursus arctos*) in the Flathead drainage between 1979 and 1991 was estimated. In the early spring, major foods included ungulates and hedysarum roots (*Hedysarum sulphurescens*). Later in the spring and early summer, green vegetation that mainly included horsetails (*Equisetum arvense*), graminoids, and cow parsnip (*Heracleum lanatum*) dominated the diet. Later in the summer, berries, particularly huckleberries (*Vaccinium* spp.) and soopolallie (*Shepherdia canadensis*), were most common. In the autumn, berries, ungulates, and hedysarum roots were major foods. Seasonal changes in nutrients were measured for major foods. The volume of a food consumed within a season was inversely related to food quality, suggesting that food availability and handling time may have been more important factors influencing diet selection. The proportions of food items in the scats, and species of fruit in particular, varied among years. The Flathead and contiguous Waterton Lakes National Park are so far the only study areas in North America that contain all major bear foods found across the interior of the continent, and in particular, both major berry species, huckleberries and soopolallie. This observation supports the hypothesis that a favourable food base in the Flathead is partially responsible for the high density of bears found there. It is important for managers to realize the possible uniqueness of the Flathead area and not extrapolate information without due caution.

Résumé : Nous avons étudié le régime alimentaire saisonnier de l'Ours brun (*Ursus arctos*) dans le bassin de la Flathead entre 1979 et 1991; plus de 1100 fèces ont été examinées. Au début du printemps, les ours mangent surtout des ongulés et des racines du sainfoin *Hedysarum sulphurescens*. Plus tard au printemps et au début de l'été, les plantes vertes, notamment des prêles (*Equisetum arvense*), des graminoïdes et la Berce très grande (*Heraclum lanatum*) prédominent dans le régime. Plus tard au cours de l'été, ce sont les petits fruits qui dominent, en particulier les airelles (*Vaccinium* spp.) et la Shepherdie du Canada (*Shepherdia canadensis*). À l'automne, petits fruits, ongulés et racines de sainfoin sont les principales composantes du régime. Les variations saisonnières des éléments nutritifs ont été mesurées dans les principaux aliments. Le volume d'un aliment consommé pendant une saison est en fonction inverse de la qualité de cet aliment, ce qui semble indiquer que la disponibilité de l'aliment et le temps nécessaire à sa manipulation influencent le choix. Les proportions des aliments dans les fèces varient d'une année à l'autre, particulièrement les diverses espèces de fruits. La Flathead et le parc national contigu de Waterton Lakes sont à ce jour les seules régions d'étude en Amérique du Nord qui contiennent tous les aliments préférés des ours sur le continent, particulièrement les deux principaux types de petits fruits, airelles et shepherdie. Ces observations confirment l'hypothèse selon laquelle la disponibilité de la nourriture préférée des ours dans le bassin de la Flathead explique partiellement la densité élevée des ours à cet endroit. Il est essentiel que les responsables de l'aménagement reconnaissent le caractère unique de la région de la Flathead et qu'ils ne procèdent pas à des extrapolations d'informations sans une certaine prudence.
[Traduit par la Rédaction]

Introduction

To understand the ecology and behaviour of grizzly bears (*Ursus arctos*), knowledge of their diet is essential (Herrero 1978). In approximately 7 months, bears must satisfy their nutritional requirements for the entire year. It is not surprising that there is a strong relationship between food quantity and quality and reproductive rates (Jonkel and Cowan 1971; Rogers 1976; Reynolds and Beecham 1980; Bunnell and Tait 1981; Kolenosky 1990), and some populations appear to be ultimately regulated by food (McLellan 1994).

A long-term investigation of grizzly bear ecology was initiated in 1978 in the Flathead River drainage in southeastern British Columbia. The main objective of this study was to investigate the relationship between industrial activities and grizzly bear behaviour and population dynamics. During a

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period of intensive gas exploration and timber harvest, the grizzly bear population was at a high density, double that of any other noncoastal population studied, and yet was increasing (McLellan 1989*a*, 1989*b*). It was postulated that the quantity and diversity of food in the study area were relatively favourable and permitted the grizzly bear population to prosper in spite of the human activity.

In this paper we document the grizzly bear diet and changes in nutrients of major foods in the Flathead study area. Because food biomass and production have not been measured in other study areas, we cannot test the hypothesis that the Flathead has a better food base; however, we can compare the diversity of foods of various qualities used by Flathead bears with those used by other populations.

Study area

The study was performed in the North Fork of the Flathead River drainage in British Columbia and Montana (49°N; 114°85′W) and covered approximately 3000 km^2. The river flows from about 1340 to 1220 m through a wide, flat-bottomed valley with rolling hills. On either side of the valley, subranges of the Rocky Mountains rise to over 2800 m.

Wildfires in the late 1800s and early 1900s burned much of the study area. Later, beetle infestations (*Dendroctonus ponderosae* and *D. obsesus*) killed many trees, which were then harvested by clear-cutting. During the study, the valley was a mosaic of young, nonmerchantable lodgepole pine (*Pinus contorta*), immature larch (*Larix occidentalis*), and subalpine fir (*Abies lasiocarpa*), low-gradient riparian areas, marshes and dry meadows, and numerous clearcuts and roads. Forests in mountainous areas contained mixtures of spruce (*Picea engelmannii* × *glauca*), subalpine fir, white-bark pine (*Pinus albicaulis*), and alpine larch (*Larix lyallii*). Early successional burns, snowchutes, alpine meadows, selective cuts and clearcuts, roads, and rock outcrops were also common in the mountains.

There was a great diversity of mammals in the study area that were potential foods and (or) competitors of grizzly bears. Moose (*Alces alces*), mountain goats (*Oreamnos americanus*), and some elk (*Cervus elaphus*) occurred in the study area throughout the year. White-tail deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and most elk appeared to migrate into the study area in spring but wintered elsewhere. Beaver (*Castor canadensis*) and ground squirrels (*Spermophilus columbianus*) were common. Other large carnivores included cougar (*Felis concolor*), wolf (*Canis lupus*), and black bear (*Ursus americanus*).

Methods

Diet contents

Between 1978 and 1991, 77 different grizzly bears were radio-collared in the study area and relocated using aerial and ground-based telemetry methods. Scats were collected during field investigations of radiolocation sites, on roads, and at trap sites. Because of the abundance of black bears and potential biases in the collection of scats (Mattson et al. 1991), guidelines for collection were established. A maximum of 2 scats was collected from roads per day and only if tracks clearly indicated the species of bear. Based on this criterion and our frequent use of the road network, scats collected from roads were usually less than 1 day old. Approximately 25% of the scats were collected on roads.

Scats were collected at radiolocation sites shortly after the bears had moved away and only if the scat size and age matched those expected from the focal animal. If 1 or 2 scats were found at a telemetry site, they were collected, but more than 5 scats were needed if the maximum per site, 3, were collected. Scats encountered while hiking to a radiolocation site were only collected if associated tracks indicated that the scat was from a grizzly bear. Based on these guidelines, a sample of 1100 scats was collected, most (73%) at or while hiking to telemetry sites, and all were estimated to be less than 1 week old.

Because of unequal funding levels and study emphasis within and among years, scat collection varied with time. The number of scats collected was highest in July and August, when little emphasis was put on trapping bears, and lowest in April and November, when many bears were denned and snow hampered fieldwork. Similarly, most scats were collected between 1980 and 1985, when this aspect of the bears' ecology was emphasized.

Methods for analyzing scat content were the same as described by Mattson et al. (1991) and were conducted at the same laboratory. Because scat analysis in the laboratory yielded the same results as field analysis of scats containing only huckleberries with <5% ants, some huckleberry scats were analyzed in the field. Bear foods were grouped into the same categories or "food items" as those of Mattson et al. (1991). To reflect seasonal shifts in foods consumed, the frequency of occurrence and the percentage of total volume of taxonomic units of food items in scats from all years were recorded for weekly and biweekly periods. Dates of seasonal changes were recorded as the week when a new food group had a higher mean percent volume than the food group that was dominant during the previous season.

Changes in nutrients of major foods

Depending on their size, 10 to several hundred individual plants of major vegetative bear foods were collected and grouped for nutrient analysis in locations frequently used by grizzly bears for feeding. Samples of horsetails (*Equisetum arvense*), cow-parsnip (*Heracleum lanatum*) leaves and stalks, and graminoid foliage were collected over approximately 1-ha areas in riparian and snow-chute habitats at biweekly intervals from late May to mid-September. Hedysarum (*Hedysarum sulphurescens*) roots were collected in clearcuts, timber adjacent to the clearcuts, and along the floodplain of the Flathead River at monthly intervals between mid-June and mid-October. Peavine (*Lathyrus ochroleucus*) was collected monthly between mid-June and mid-August in clearcuts. Soopolallie (*Shepherdia canadensis*) was collected in a burn in August, while huckleberries (*Vaccinium membranaceum*) were collected during August at two elevations and under conifer canopy of different densities. Glacier lily (*Erythronium grandiflorum*) bulbs were collected during July under an alder (*Alnus sinuata*) canopy in a snow chute.

Nutrient analysis followed methods described by Pritchard and Robbins (1990). Gross energy and nitrogen content were determined with bomb calorimeter and macro-Kjeldahl methods. Ether extract was estimated using a Soxhlet apparatus. Total dietary fiber was determined by the enzymatic–

Fig. 1. Annual trends in the volume of residue of various food items found in grizzly bear scats collected in the Flathead drainage of British Columbia and Montana between 1979 and 1991.

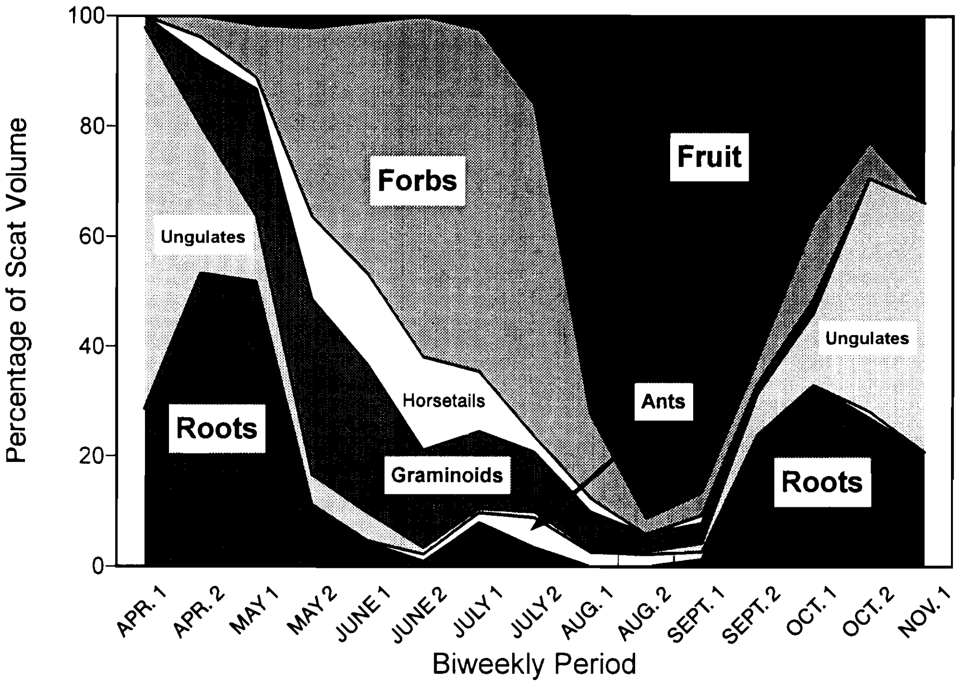


Table 1. Percent volume and percent occurrence (in parentheses) of major food items in grizzly bear scats collected in the Flathead drainage, 1979–1991.

	n	Ungulates	Ants	Roots	Graminoids	Horsetails	Forbs	Fruit	Rodents
Early April	8	61 (63)	0	25 (25)	2 (13)	0	0	0	1 (1)
Late April	20	24 (35)	0.6 (15)	48 (55)	11 (20)	3 (5)	4 (20)	0	0
Early May	61	11 (18)	0.1 (2)	48 (56)	21 (44)	2 (5)	9 (20)	1 (3)	0.4 (2)
Late May	94	5 (18)	0.2 (4)	10 (15)	30 (67)	14 (30)	32 (62)	2 (4)	2 (4)
Early June	92	5 (13)	0.4 (9)	4 (4)	26 (52)	16 (36)	44 (67)	1 (1)	0.8 (4)
Late June	92	1 (7)	1 (17)	1 (2)	17 (46)	16 (32)	59 (76)	0	0.8 (3)
Early July	130	0.8 (2)	2 (17)	8 (10)	13 (36)	11 (25)	60 (82)	2 (8)	0.6 (1)
Late July	129	1 (4)	5 (36)	3 (5)	10 (28)	3 (6)	57 (73)	15 (28)	0.3 (2)
Early August	113	0.5 (4)	3 (30)	0	7 (23)	2 (7)	15 (26)	71 (88)	0.1 (1)
Late August	132	0.5 (2)	2 (17)	0	3 (17)	0	3 (7)	89 (96)	0
Early September	69	2 (3)	1 (16)	1 (4)	4 (10)	1 (1)	4 (6)	86 (93)	0
Late September	64	7 (13)	0.2 (5)	23 (28)	2 (14)	0	4 (13)	60 (66)	0.3 (3)
Early October	49	12 (25)	0.1 (2)	32 (38)	2 (8)	0.4 (2)	13 (16)	36 (41)	0
Late October	38	38 (47)	1 (3)	25 (32)	0	0	6 (8)	21 (24)	0
Early November	11	40 (46)	0	18 (18)	0	0	0	30 (36)	0

gravimetric method described by Prosky et al. (1984), which is considered the preferred method for animals with minimal fermentative capability (Pritchard and Robbins 1990). Equations produced by Pritchard and Robbins (1990) were used to calculate apparent digestible energy and apparent digestible protein.

Arcsine conversions of mean percent scat volume were related to apparent digestible energy and apparent digestible protein using multiple regression. Nutritional data used as independent variables were averages among collection sites. Scat volumes used as the dependent variable included scats collected over the 2-week period that encompassed the collection date for nutrient analyses. For these analyses, data were pooled from within late-spring and within late-summer seasons.

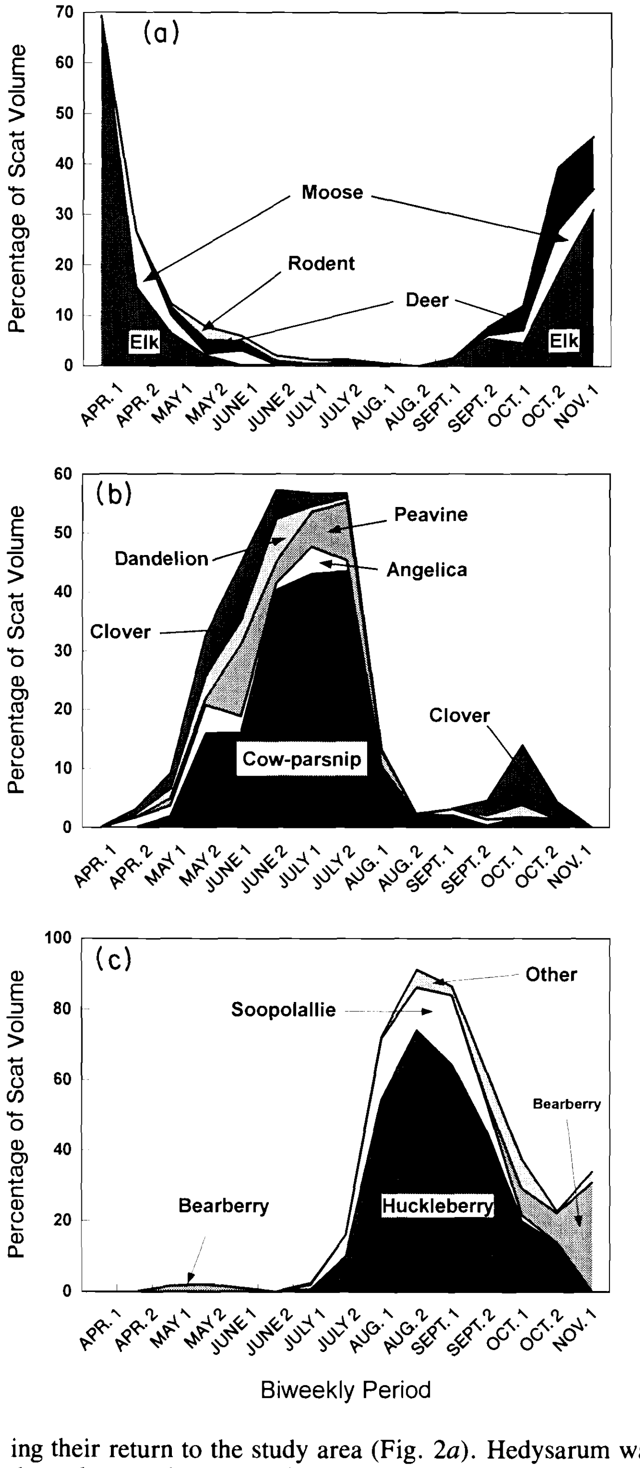
Results

Seasonal diet changes

Almost all scat contents could be placed in the same categories as those used by Mattson et al. (1991); however, only 8 were required (Table 1). Although spawning trout (*Salmo clarki*), white-bark pine, and mushrooms (Basidiomycotina) were common in the study area, these categories were excluded from our analyses because they did not occur in the scat sample, although we observed one case of apparent feeding on pine nuts. Only 2 of the 1100 scats contained garbage so this category was also excluded.

In April and early May, ungulates and roots dominated the bears' diet (Fig. 1). Elk and moose were found in the April sample, while deer first occurred in early May, reflect-

Fig. 2. Annual trends in the volume of residue from various species of mammals (*a*), forbs (*b*), and fruits (*c*) found in grizzly bear scats collected in the Flathead drainage of British Columbia and Montana between 1979 and 1991.



ing their return to the study area (Fig. 2*a*). Hedysarum was the only root in the April sample. Ungulate and root use declined in mid-May, when the contribution of green vegetation increased. Use of graminoids gradually increased from late April and peaked in late May at 32% of scat volume.

Bears' use of forbs followed use of graminoids by about 2 weeks, increasing from early May to a plateau of 60–62% of the scat volume between late June and the end of July. Cow-parsnip represented 59% of the total volume of forbs during this period (Fig. 2*b*). Other forbs with notable volume included peavine, clover (*Trifolium* spp.), angelica (*Angelica arguta*), and dandelion (*Taraxacum* spp.). Small volumes of glacier lily bulbs also occurred in the July sample.

Although a small volume of overwintered bearberry (*Arctostaphylos uva-ursi*) was found in May scats, fruit did not become prominent until late July, when soopolallie and huckleberries became available (Fig. 2*c*). These, particularly huckleberries, dominated the scat volume until late September, when elk, moose, and deer plus hedysarum roots again became significant. These foods remained common in the scats until bears denned. Reduced use of huckleberries continued until late October, and other fruits such as bearberry, cranberry (*Viburnum edule*), and rhamnus (*Rhamnus alnifolia*) increased in significance. There was a noted increase in use of clover in October.

Based on shifts in the diet of grizzly bears in the Flathead drainage, four seasons were identified for the active part of the year. Roots and ungulates dominated the diet of grizzly bears during the early-spring or pre-green-up season that ended between weeks 2 and 3 of May. Green vegetation then dominated the diet in the late-spring season until the end of July, when fruit became more voluminous in scats than greens. The late-summer or berry season continued until week 4 of September, when an increase in roots and ungulates in the scats marked the beginning of autumn, which ended when the bears hibernated.

Differences among years

Although considerable variation in scat content was noted among years, forbs were always the dominant food item during late spring and these were followed by either graminoids or horsetails (Table 2). Cow-parsnip was the most abundant species in late-spring scats each year from 1980 to 1985, but clover was more abundant during 1989 and 1991.

Fruits were always the most abundant food item in late-summer scats (Table 2) but there was inconsistency in the contribution of genera. In late summer 1981, soopolallie was most common, while in late summer 1983, 90% of the scat volume consisted of huckleberries and only 2% was soopolallie. Scat contents were very similar in autumn during 1982 and 1983 but during 1979, fruits and ungulates were almost absent (Table 2). Clover was common in the scats collected during the autumn of 1979 but rare in scats from 1982 and 1983.

Changes in nutrients of major foods

The apparent digestible energy (ADE) and protein (ADP) of late-spring foods decreased from late May, when the first samples were collected, through the spring and summer (Table 3). Of the late-spring green vegetation foods, cow-parsnip had the highest ADE and ADP during each sample period; moreover, these high levels were maintained throughout the late-spring season. Peavine also maintained its quality longer than grasses or horsetails. Glacier lily bulbs were higher in ADE than green vegetation foods, but low in ADP. Animal food, such as ungulates, were much higher in both ADE and ADP than were plant foods.

Of the plants collected in any season, soopolallie, followed by huckleberries and glacier lily bulbs, contained the highest ADE. The ADE and ADP of hedysarum increased from June, when it was first collected, to mid-September.

Table 2. Percent volume of food items during years when at least 20 scats were collected during late spring, late summer, and autumn.

			Food					
	Year	*n*	Ungulates	Roots	Graminoids	Horsetails	Forbs	Fruit
Late spring	1980	64	4.1	8.3	25.6	16.9	35.3	0.2
	1981	98	1.1	1.8	27.2	17.0	47.3	1.4
	1982	69	4.9	12.7	11.1	7.4	54.5	4.1
	1983	81	2.4	5.6	18.9	6.0	60.3	1.5
	1984	51	1.8	1.8	19.7	17.3	56.9	0.6
	1985	36	3.1	3.9	19.6	2.0	64.8	6.0
	1989	23	2.8	1.1	8.2	9.7	56.7	7.5
	1991	21	0.1	6.9	11.4	16.7	59.2	0.0
Late summer	1981	66	0.7	1.5	10.2	2.4	12.0	68.6
	1982	68	0.9	1.5	5.3	2.7	15.5	67.4
	1983	168	0.3	0.0	1.5	0.0	1.7	93.0
	1984	30	2.5	0.0	1.5	3.0	31.2	58.0
Autumn	1979	20	5.0	47.0	6.5	0.0	36.4	0.4
	1982	36	27.1	16.7	0.7	0.6	5.8	37.1
	1983	33	23.7	37.7	1.5	0.0	1.4	32.8

Note: Only food items composing at least 5% of the volume during any season in at least one year are included.

Table 3. Average apparent digestible energy (ADE; kJ/g dry matter) and percent apparent digestible protein (ADP) of major spring foods collected at grizzly bear feeding areas in the Flathead drainage, 1991.

		Date (month-day)								
		5-31	6-14	7-01	7-15	8-01	8-15	9-03	9-16	10-18
Horsetails (*n* = 2; snow chute and riparian)	ADE	5.9	5.1	4.9	5.2	4.9	5.1	4.3	4.0	
		(0.31)	(0.15)	(0.07)	(0.31)	(0.27)	(0.41)	(0.14)	(0.51)	
	ADP	22.6	17.8	11.7	8.5	6.9	5.5	2.8	1.9	
		(0.96)	(2.57)	(0.69)	(0.41)	(1.17)	(0.45)	(1.65)	(1.00)	
Grasses (*n* = 2; snow chute and riparian)	ADE	5.3	4.1	2.6	3.0	1.7	2.0	2.1	2.6	
		(1.60)	(0.55)	(0.40)	(0.86)	(0.31)	(0.59)	(0.35)	(0.09)	
	ADP	20.9	16.6	12.3	10.7	8.8	7.3	5.5	5.4	
		(3.20)	(0.38)	(2.20)	(0.39)	(0)	(0.76)	(0.06)	(1.15)	
Cow-parsnip (*n* = 2; snow chute and riparian)	ADE	8.6	8.0	8.1	8.3	8.1	7.9	6.8	6.0	
		(0.09)	(0.46)	(0.22)	(0.45)	(0.73)	(0.19)	(0.59)	(0.37)	
	ADP	25.5	19.5	14.9	12.3	12.6	11.7	9.0	6.3	
		(0.90)	(2.18)	(0.31)	(2.92)	(2.26)	(0.27)	(1.50)	(1.00)	
Peavine (*n* = 1, clearcut)	ADE		6.6		6.7		5.4			
	ADP		15.0		12.9		9.2			
Hedysarum (*n* = 3; forest, clearcut and floodplain)	ADE		4.7		5.3		6.3		7.3	7.2
			(1.64)		(0.69)		(1.31)		(1.70)	(0.87)
	ADP		5.7		4.95		6.3		7.0	8.1
			(1.63)		(1.57)		(2.07)		(1.67)	(0.15)
Huckleberries (*n* = 3; open timber and open burns)	ADE						13.0	12.9		
							(0.25)	(0.31)		
	ADP						0.2	0.1		
							(0.34)	(0.14)		
Soopolallie (*n* = 1; burn)	ADE						15.7			
	ADP						6.3			
Glacier lilies (*n* = 1; snow chute)	ADE				10.1					
	ADP				4.7					
Deer[a]	ADE	29.0								
	ADP	40.4								

Note: Numbers in parentheses show the standard deviation.
[a]Data from Pritchard and Robbins (1990).

Multiple regression indicated a negative relationship between the average percent volume of foods in scats and the ADE and ADP of these foods during late summer (R^2 = 0.50, $P < 0.001$) and possibly late spring (R^2 = 023, P = 0.09). Availability and handling time of each food type appears to play a greater role in the diet of grizzly bears than ADE and ADP. When ungulates, whose availability to bears is relatively low, and glacier lily bulbs, which are inefficiently handled, were excluded from the data, there was a significant relationship between the average percent volume in scats and the ADE and ADP of these foods in late spring ($R^2 = 0.33$, $P = 0.02$) and late summer ($R^2 = 0.61$, $P < 0.001$). During late spring, coefficients for both ADE and ADP were positive; however, the coefficient for ADP was negative during the late summer.

Discussion

Bias and error

The quantitative assessment of a grizzly bear diet on the basis of scat analysis is subject to four types of error. First, each scat deposited may not have an equal chance of being collected. In rugged, mountainous terrain, particularly where vegetation is dense enough to make human travel and the detection of scats difficult, scat collection can be biased towards where people go and where scats are easily found. Such areas are often at low elevations, on gentler terrain, in open habitats, and, in particular, along roads and trails. Additionally, some scats, such as those dominated by ants, are more cryptic and thus more difficult to find than those containing colourful foods such as berries. Scats associated with more obvious bear sign, such as diggings for roots or bear trails through tall forbs, are easier to locate than scats not associated with obvious sign, such as those deposited by a grazing animal. In the Flathead study site, 73% of the scats were collected at or while hiking to locations of radio-collared grizzly bears, which reduced but is unlikely to have eliminated this bias.

With more black bears than grizzly ears in the study area, the second potential source of error is the collection of scats from the wrong species. Again, reliance on telemetry locations plus the strict criterion of discriminating sign minimized this problem.

The third source of error is that the volume of fecal residue produced after consumption of a given amount of food varies among foods. The extent of this variation depends on both the digestibility of the food and the proportion of fecal residue that is both recognizable and recoverable during analysis. For an omnivore with a highly variable diet, this bias could be significant. Although at this time we cannot quantify the bias, highly digestible foods such as meat and berries would constitute a greater proportion of the diet than is suggested by scat analysis, while the opposite would be true for less digestible foods such as roots and graminoids.

The fourth source of error may be due to variation in scat sizes. If each scat is considered to contribute equally to the composite data, then food items that tend to be found in small scats will be overestimated and items that tend to be found in large scats will be underestimated. To avoid this bias, the volume of each scat should be used to weight that scat's contribution to the composite data. Because of the amorphous nature of many scats, it is difficult, if not impossible, to measure the volume of all scats collected in the field. The extent of this bias has not been quantified; however, our observations suggest that scats from bears feeding on highly digestible foods such as berries tend to be smaller than those from bears feeding on less digestible foods.

Seasonal diet changes

Classical foraging models suggest that availability, handling time, and quality largely predict what foods animals should eat (Krebs and McCleery 1984). The negative relationship between food quality and volume consumed suggests that availability and handling time have a great influence on forage selection by bears. Food availability may be a more significant factor in diet selection by omnivores than by other animals because their foods vary between rare, high-quality animal matter and abundant, lower quality vegetation.

Prior to green-up, hedysarum roots and winter-killed or weakened ungulates are the major foods available to bears. Although the ADE of dormant hedysarum is higher than that of graminoids and horsetails, bears generally switch to the greens when they become available. Not only does the quality of hedysarum decrease as energy stored in the roots goes into vegetative growth, but the handling time of green vegetation is likely much less than that required for digging roots.

Mammals are the food of highest quality throughout the year but the proportion of mammals in the diet of grizzly bears decreased after green-up. This decrease may reflect both a reduction in the effort spent searching for ungulates, owing to the relative abundance of green vegetation plus a decrease in ungulate availability. Ungulate neonates provided some animal food in late May and June, as has been reported elsewhere (Hamer and Herrero 1987, 1991; Gunther and Renkin 1990; French and French 1990), but a pulse of use was not detected in the scats of Flathead area bears. We suspect that feeding on neonates in late May and early June followed feeding on winter-weakened adult ungulates close enough that we did not detect an increase in consumption of mammals in late May.

The decline in use of graminoids and horsetails and the increase in the use of forbs in late June and July may reflect the continued high levels of ADE and ADP in forbs but not in the other greens. When berries ripened near the end of July, bears made an abrupt switch to these fruits, which had a higher level of ADE than any of the green vegetation but a lower ADP level. The decrease in bears' use of berries in late September coincides with the decreasing availability of this food. The increase in use of ungulates in the autumn appears to be due to a decrease in the availability of berries and an increase in available ungulates during the sport hunting season.

Variation among years

Hamer and Herrero (1987) and Mattson et al. (1991) demonstrated considerable interannual variation in foods used by grizzly bears. Mattson et al. (1991) found that after 11 years of data collection, new and significant foods were still evident and they stressed the potential for error if bear diets are inferred from only a few years of data. Our results support this conclusion; however, human activities appear to have influenced some changes in diet. Clover was relatively rare in the late-spring diet of grizzly bears until 1989, when it became abundant after being seeded along seismic lines and gas-drilling sites throughout the study area. Heavy use of clover during the autumn of 1979 was due to seeding of logging landings in the 1970s plus a lack of huckleberries that year. The abundance of clover decreased in these landings shortly after 1979 and bears' use of it during autumn was reduced.

Most interannual variation in natural foods consumed results from changes in fruit abundance. Production of both huckleberry and soopolallie berries varies greatly among years (Martin 1983; Hamer and Herrero 1987; B.N. McLellan and F.W. Hovey, unpublished data) and this variation was reflected in the species consumed. With two major fruiting species plus several others of less prominence, simultaneous failure of all fruits is rare in the Flathead study area.

Comparisons among study areas

The estimated density of grizzly bears in the Flathead drainage was higher than in other interior study areas (McLellan 1989*a*). Only on coastal Alaska, where spawning salmon (*Oncorhynchus* sp.) are abundant, are density estimates higher. McLellan (1989*a*) postulated that in the quantity and diversity of foods, the Flathead drainage was superior to other interior study areas and this result contributed to the high bear density. Owing to a lack of data, food quantity cannot be compared among areas; however, some generalizations concerning the diversity of foods consumed by various populations can be made.

Although many foods are eaten by bears in the Flathead study area, most of the energy and protein used by the population is produced by a few. These major foods include (*i*) ungulates, of which there are six species, (*ii*) hedysarum, which grows in various locations from the floodplain to mountain ridges, (*iii*) green vegetation, particularly horsetails, graminoids, and cow-parsnip, and (*iv*) fruits of many species, huckleberries and soopolallie being the most productive.

In a summary of grizzly bear food habits, LeFranc et al. (1987) concluded that graminoids, horsetails, cow-parsnip, clover, dandelions, hedysarum, huckleberries, and soopolallie are the dominant plant foods over large portions of the interior of North America. All of these major foods are abundant in the Flathead study area.

The diets of grizzly bears in other portions of the Canadian Rocky Mountains were similar to that of Flathead bears, but, there were important differences. In Banff and Jasper National Parks, grizzly bears relied more on hedysarum roots than did Flathead bears (Russell et al. 1979; Hamer and Herrero 1987). Flathead bears also ate much more cow-parsnip and huckleberries, which were both rare in these parks. After 3 years of research in Waterton National Park, which is contiguous with the Flathead study area and used by some radio-collared bears, Hamer et al. (1991) reported only huckleberries to be a major fruit in the bears' diet, with soopolallie constituting less than 2% of the scat volume in any semimonthly period. Because soopolallie plants are abundant in Waterton National Park, it is likely that a longer study would find heavier use of these berries in some years.

Bears in Yellowstone National Park ate little fruit of any species (Mattson et al. 1991), and on the East Front of Montana, huckleberries are rare (Aune and Kasworm 1989). In both of these areas, white-bark pine seeds are an important autumn food. Although white-bark pine are common in the Flathead study area, we have only once found evidence of bears eating their seeds, and none have been found in the scats. In the Mission Mountains (Servheen 1983) and South Fork of the Flathead River (Mace and Jonkel 1986), hedysarum and soopolallie are rare or absent.

Unlike research on southern grizzly bears, studies in more northerly latitudes have focused more on population characteristics than on habitats and foods; however, some qualitative information is available. Not only is the growing season short in northern areas, the diversity of major bear foods was generally less than in the Flathead area. Forbs of any kind, and huckleberries in particular, were notably rare in the diet of most northern bears (Pearson 1975; Reynolds 1976; Miller et al. 1982; Nagy et al. 1983*a*, 1983*b*).

It appears that bears in the Flathead area and neighbouring Waterton Lakes National Park are the only ones so far studied in southern parts of the continent that have all major interior bear foods available to them. In particular, both huckleberries and soopolallie are present and abundant enough that either can dominate the late-summer diet if the other fails to produce. Without being able to compare food abundance, however, we cannot conclude that the high density of bears in the study area is due to better foods. We do caution managers, however, that the Flathead area, with its high density of bears, may not be representative of many interior areas, and extrapolation without additional field investigations should be avoided.

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