Food habits of Yellowstone grizzly bears, 1977–1987

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Food habits of grizzly bears were studied for 11 years in the Yellowstone area of Wyoming, Montana, and Idaho by analyzing scats. Ungulate remains constituted a major portion of early-season scats, graminoids of May and June scats, and whitebark pine seeds of late-season scats. Berries composed a minor portion of scats during all months. The diet varied most among years during May, September, and October, and was most diverse during August. Defecation rates peaked in July and were low in April through June. Among-years differences in scat content were substantial; estimates of average scat composition took 4–6 years to stabilize. Major trends in diet were evident and reflected long-term variation. We suggest that long-term studies are necessary to adequately document bears' food habits in variable environments; the Yellowstone grizzly bears' diet varied with seasonal and yearly availability of high-quality foods, lack of berries and large fluctuations in the size of pine seed crops were major factors limiting bear density in the Yellowstone area, and the availability of edible human refuse buffered the limitations imposed by inadequate berry and pine seed crops prior to the 1970s.

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Les habitudes alimentaires ont été étudiées par analyse des fèces durant 11 ans chez des Ours Bruns de la région de Yellowstone du Wyoming, du Montana et de l'Idaho. En début de saison, les fèces contenaient surtout des ongulés: en mai et juin, ce sont les graminoïdes qui dominaient dans les fèces et en fin de saison, ce sont les graines du Pin albicaule. Il y avait toujours une petite portion de petits fruits dans le fèces à tous les mois. Les différences alimentaires d'une année à l'autre étaient marquées surtout en mai, septembre et octobre et c'est en août que le régime etait le plus diversifié. Les taux de défécation étaient maximaux en juillet et faibles d'avril à juin. Le contenus des fèces variaient considérablement d'une année à l'autre; la composition moyenne des fèces ne devenait stable qu'après des estimations de 4–6 ans. Les résultats indiquent qu'il existe des tendances alimentaires bien définies et mettent en lumière une variation à long terme. Il semble donc que seules des études à long terme puissent permettre de déterminer adéquatement les habitudes alimentaires des ours dans des milieux variables; le régime alimentaire des Ours bruns de Yellowstone varie en fonction de la disponibilité saisonnière et de la disponibilité annuelle des aliments de qualité; l'absence de petits fruits et les fluctuations importantes de l'abondance des graines de pins constituent d'importants facteurs limitants de la densité des ours dans la région de Yellowstone; la disponibilité de rebuts humains comestibles parvenait à compenser la pénurie de petits fruits et de graines de pins avant les années 1970.

[Traduit par la rédaction]

Introduction

The Interagency Grizzly Bear Study Team has been studying grizzly bear ecology in the Yellowstone area since 1973. Collection of information and fecal matter (scats) from sites used by bears has been a study priority. Collection of scats has continued from our study's inception to the present (1973–1988), since 1976 in conjunction with a more integrated habitat data collection effort involving radio-collared animals.

In three previous studies, grizzly bear food habits in the Yellowstone area were investigated. Murie (1944) reported 1 year's scat data, from 1943, collected principally from bears observed in campgrounds and along highways in Yellowstone Park. Drs. John Craighead and Frank Craighead, Jr. have mentioned the results of food-habit investigations from their 1959–1970 study in Yellowstone Park (e.g., Craighead and Craighead 1972; Craighead and Mitchell 1982; Craighead et al. 1982), but have not yet presented complete results. Mealey (1980) analyzed grizzly bear scats collected during 1973 and 1974 in Yellowstone Park; these data did not involve radio-collared animals.

These earlier studies of grizzly bear food habits in the Yellowstone area probably have limited application to the current situation. In all three studies, data collection was focused in Yellowstone National Park; however, a major portion of the contemporary grizzly bear population ranges outside the park (Basile 1982; Knight and Eberhardt 1985). Murie's study was oriented toward bears operating in close proximity to humans. The Craigheads' data are likely to have limited current application because their study bears tended to concentrate around garbage disposal sites in June through August, feeding on human refuse (Craighead and Craighead 1971). Mealey's study was complicated by biases inherent in scat collection without the aid of telemetry and studying a population in transition from feeding at or near garbage disposal sites during a significant portion of the year to feeding in a way that is much less influenced by humans. In addition, the short studies of Murie and Mealey probably did not account for among-years variation in food habits.

In this paper we present an analysis of Yellowstone grizzly bear scat contents, using scats collected in 1977–1987. We focus on seasonal and among-years variation in scat contents and its relevance to food habit studies and grizzly bear management.

Study area

Our study area, covering 20 000 km^2, includes Yellowstone National park and surrounding national forests. Elevations range from 1600 to 3300 m over extensive central plateaus surrounded by higher relief mountains. The climate is characterized by long cold winters and short cool summers, annual temperatures over most of the study area averaging 0–4°C. Annual precipitation averages 60 cm and ranges between 35 and 100 cm geographically. Most precipitation above 2100 m elevation occurs as snow (Dirks and Martner 1982).

The study area is primarily in the subalpine zone and mostly (75%) forested. Much of this forest consists of lodgepole pine (*Pinus contorta*) dominated stands, although Douglas-fir (*Pseudotsuga menziesii*),

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TABLE 1. Percent volume (%V) and index of among-years variation in volume (R_V) for diet items in scats, averaged among study years by month,

	April–May			April			May		
	%V	R_V	SV	%V	R_V	SV	%V	R_V	SV
Ungulates (domestic livestock)									
(Ungulata)	28.1	−0.14	67.3	48.5	−0.39	75.6	16.8	0.09	60.1
	(t	—	3.0)	(0	—	—)	(t	—	3.0)
Rodents (Rodentia)	3.4	−0.09	48.3	2.2	−0.20	37.2	3.5	0.21	58.0
Cutthroat trout (*Oncorchynchus clarki*)	0.5	1.12	32.9	t	—	10.0	1.0	1.14	34.0
Insects (Insecta)	2.6	0.10	14.9	1.1	0.01	24.9	3.6	−0.15	13.0
Horsetail (*Equisetum* spp.)	2.5	0.02	33.6	0	—	—	3.3	−0.04	33.6
Graminoid foliage (Graminales)	41.2	−0.16	67.4	20.5	−0.05	62.1	46.3	0.02	68.6
Forb foliage (Dicotyledoneae)	4.7	−0.41	27.6	4.6	−0.97	35.6	3.9	−0.31	26.3
Forb and graminoid roots (Dicotyledoneae									
and Graminales)	4.0	−0.25	52.4	6.6	−0.11	72.3	3.6	−0.13	41.7
Fleshy fruits (Dicotyledoneae)	1.5	0.13	53.7	0	—	—	2.0	0.05	53.7
Whitebark pine seeds (*Pinus albicaulis*)	1.1	0.11	92.3	0	—	—	9.9	1.07	92.3
Mushrooms and puffballs (Basidiomycotina)	0	—	—	0	—	—	0	—	—
Garbage	0.2	−0.25	12.7	0.2	−0.45	30.0	0.3	0.09	9.8
Debris	9.0		23.8	3.7		23.0	4.9		24.9
No. of years		7			3			7	
No. of scats		307			84			238	

NOTE: t, trace.

Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) are more common dominants on high-relief topography underlain by andesitic bedrock (Despain 1973). Extensive contiguous nonforested areas occur primarily below 2100 m, although there are occasional sizable nonforested enclaves above 2300 m. Otherwise, nonforested areas occur as rock and tundra above 3000 m or as smaller meadows in basins and on south- to east-facing slopes.

Large populations of elk (*Cervus elaphus*) and bison (*Bison bison*) and smaller populations of moose (*Alces alces*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*) occupy the study area. Yellowstone elk and bison populations were estimated at 31 000 and 2400, respectively, during our study (Singer 1988). Rodents, including pocket gophers (*Thomomys thalpoides*), voles (*Microtus* spp.), and red squirrels (*Tamiasciurus hudsonicus*), were abundant, although ground squirrels (*Spermophilus* spp.) were not.

Methods

Scats were collected while sampling or en route to and from aerial locations of radio-collared bears. Radio locations of bears throughout the study area were usually obtained once a week; two flights per week were typically required to obtain full coverage. Field crews used recreation trails as well as game trails and natural travel routes such as ridge crests. Scats were subsampled where more than five were found at one feed site. Our guidelines stipulated that all of the first set of five scats, four of the second, three of the third, two of the fourth, and one of the fifth be collected. Recognizably different kinds of scats were collected according to their representation when we subsampled. We rarely collected scats older than ca. $1^1/_2$ months. Scats were identified according to location, site and age, and association with feeding sites and radio telemetry locations.

Scats were air-dried and later rehydrated before washing through two screens. Coarse material was retained by the larger mesh (0.806 cm^2) screen and fine material by the smaller mesh (0.212 cm^2) screen. All diet items were identified to the finest taxonomic resolution possible and the percent volume of each was visually estimated. Visual estimates were routinely checked for correspondence with actual percent volumes. Scat contents were also characterized in terms of the part of the diet item, e.g., leaf, stem, flower, fruit, or root of vegetal foods. As in virtually all other studies of bear scat contents, we did not estimate total scat volumes.

Scat analysis data were summarized in terms of the frequency of occurrence of each diet item and its percent total mean volume for each year and month. Diet items were also characterized by mean percent volume in those scats in which they occurred, for each year and month. Total scat content was averaged across all years for each month, giving each year's data equal weight. Only months with year-specific sample sizes of ≥20 were used for this calculation. We used months with sample sizes <20 for constructing year-specific diagrams of scat contents.

We derived an estimate (R_V) of among-years variation in fecal volume for each diet item and month, by removing effects on the standard deviation that were attributable to the mean and sampling error. We first converted standard deviations of diet item volumes to coefficient of variation (CV), eliminating the statistical effect of the mean. A substantial relationship between mean volumes and coefficient of variation remained, which we attributed to sampling error associated with rarer diet items. We regressed the CV on arcsine conversion of mean volume (%V) to quantify this relationship. Residuals of the relationship constituted our estimate of R_V.

We calculated scat content diversity (e^H; Shannon and Weaver 1963) for each month, using scat content averaged over all years and 13 broad diet item categories. We also calculated an index of among-years variation in mean scat content for each month. This was expressed as the weighted mean of our estimate of among-years variation (R_V) over the 13 broad diet item categories, with proportionate volumes as weighting factors.

We evaluated level of grizzly bear feeding activity for each month by means of two calculations: the ratio of scats found and collected to radiotelemetry locations sampled, with the number of locations sampled serving as an index of our effort, and the proportion of sampled locations where there was no discernible sign of feeding (although tracks, scats, and beds were often found at these locations).

Results

Between 1977 and 1987 we collected 3423 scats while ground sampling 930 locations of 96 radio-collared bears. Scats were collected in March through November with varying intensity; fewer scats were collected in spring and late fall because of prohibitive field conditions and the availability of fewer personnel. We collected ≥20 scats during April for 3 years, during and mean percent scat volume (SV) (for scats in which they occurred) for diet items by month for all study years combined

June			July			August			September			October		
%V	R_V	SV	%V	R_V	SV	%V	R_V	SV	%V	R_V	SV	%V	R_V	SV
6.1	−0.46	40.9	3.1	−0.41	39.5	2.9	−0.80	40.4	4.7	−0.25	47.9	7.7	−0.16	55.0
(0	—	—)	(0.2	−0.16	70.0)	(0.2	−0.24	61.0)	(0.2	−0.32	26.7)	(0	—	—)
0.8	0.60	28.1	0.2	−0.24	19.5	0.8	−0.43	40.8	0.8	−0.35	42.2	1.1	0.33	45.1
2.3	0.40	38.0	4.4	0.31	46.4	0.5	−0.38	27.0	0	—	—	0	—	—
2.0	−0.54	11.7	7.7	0.14	17.6	7.4	0.52	25.2	1.9	−0.23	18.1	0.8	0.06	20.2
5.3	−0.38	40.7	6.6	−0.42	37.8	1.2	0.31	3.1.	0.5	0.07	24.5	0.1	−0.35	20.0
41.9	−0.26	61.3	27.8	−0.29	41.3	22.4	−0.17	47.8	14.3	−0.16	44.6	12.3	−0.31	44.3
18.4	−0.19	46.4	25.2	−0.37	48.5	17.2	−0.11	46.2	6.8	−0.08	41.0	4.6	0.43	38.8
4.3	−0.03	42.7	7.2	0.04	2.7	7.3	−0.48	51.0	12.1	0.40	68.2	19.3	0.53	68.2
0.4	−0.15	16.2	0.8	−1.02	11.5	9.4	−0.08	52.1	5.2	0.03	54.9	3.8	0.15	31.6
12.9	0.41	86.1	8.8	0.50	66.3	17.6	0.70	87.1	39.0	0.23	89.5	39.2	0.39	91.6
0	—	—	t	—	3.0	0.2	−0.65	27.1	2.0	0.21	39.9	t	—	15.5
0.1	−0.79	5.6	1.2	−0.03	35.7	2.7	0.37	75.2	1.2	0.64	56.0	0.4	0.11	36.8
3.8		23.8	6.5		28.8	8.1		33.2	9.1		32.5	5.6		38.3
	9			9			9			7			5	
	696			987			787			499			340	

October for 5 years, during May and September for 7 years, and June through August for 9 years. During the summers of 1984 and 1985 we intensively ground-tracked a few radio-collared bears. Scats for this period were not included in the sample of 3423, but were used to construct year-specific diagrams.

Virtually all the scat material could be included in 13 broad categories (Table 1). Material not covered by these categories included such things as trap bait and birds. In contrast to dicotyledons and mammals, we were rarely able to identify graminoid and insect species from scats. In virtually all instances where we were able to identify graminoid species, they were characteristic of mesic sites, e.g., *Carex raynoldsii, C. praticola, Bromus anomalous, Agropyron caninum*, and *Phleum alpinum. Festuca idahoensis* was also identified occasionally. Recognition of these species was aided by their propensity to flower and set fruit. Nine species of ants were identified in scats, the majority belonging to the genera *Camponotus and Formica*, most commonly *Camponotus pennyslvanicus modoc* and *Formica neorufibarbis*. We also identified army cutworm moths (*Euxoa auxiliaris*) in scats collected during 1987.

Scat contents over all years averaged

The greatest use of mammals by bears occurred during spring and fall (Table 1). Ungulates constituted nearly half of the fecal matter in April, and mean percent scat content was high, especially during April, May, and October. Virtually all early-season ungulate use was of winter-killed or weakened animals, whereas late-season use was primarily of bulls weakened by the rut. Rodents composed a minor portion of the diet, although mean percent scat content was relatively high during spring and late summer and fall. Voles and pocket gophers were used primarily, often coincidental to the excavation of their root caches.

Other animal foods exhibited midseason peaks in volume. Cutthroat trout was used in greatest volumes during June and July, concurrent with peak mean percent volume in scats. Trout were used almost wholly while spawning in streams entering Yellowstone Lake. Peak use of insects, principally ants (Formicidae), occurred in July and August, though insects were distinguished by the lowest means percent volume of any diet item; they were primarily obtained by excavating worker ants and pupae from nests in logs and debris hills.

Mushrooms and puffballs constituted a minor portion of scat volume, with peak representation in September. Mean percent volume was moderate to low and paralleled mean total scat volume. Basidiocarps were foraged primarily in drier lodgepole pine forests.

Horsetails, principally *Equistem arvense*, composed a substantial portion of scat volume during peak use in June and July. Mean percent scat volume was moderately high during an overlapping but extended period, from May through July. Horsetails were primarily obtained by grazing stems in characteristic wet sites.

Graminoids composed a major portion of fecal matter in May and June, and were used in substantial volumes during the other months. Mean percent scat volume was generally high, in the same range as for ungulates, and paralleled mean total scat volume. Among identifiable genera, bluegrass showed an early-season peak and sedge a late-season peak in use. Graminoids were grazed, and were represented in the scats mostly by leaves. Most graminoid scat material was categorized as "grass–sedge," owing to the prevalence of leaves and the corresponding lack of identifying inflorescences.

There were substantial amounts of grazed forbs in scats during all months, but their use peaked in July, 2 months later than that of graminoids. Spring beauty (*Claytonia lanceolata*), fireweed (*Epilobium angustifolium*), and salsify (*Tragopogon dubius*) were minor scat components, whereas dandelion (*Taraxacum* spp.) was present in substantial volumes; other forbs occurred in intermediate amounts. Representation of most individual forb species peaked in July, although dandelion was distinguished by an earlier (June) peak, and clover (*Trifolium* spp.) by a later (August) peak. Bears used elk thistle (*Cirsium scariosum*) primarily during July, after the stem had bolted, first removing most of the spiny leaves and inflorescences.

Fecal volumes of excavated forbs and graminoids peaked in

September and October and to a lesser extent in April. Mean percent scat volumes of roots were moderately high or high during all months. The late-season peak in use corresponded to the excavation of individual roots, and the early-season peak to excavation of pocket gopher root caches. The onion-grass (*Melica spectabilis*) bulbs common in April, May, and October scats were derived almost exclusively from rodent caches. Sweet cicely (*Osmorhiza* spp.), pondweed (*Potamogeton* spp.), and yampa (*Perideridia gairdneri*) all received peak use in September and October, although yampa also received substantial use during July and August. Biscuitroot (*Lomatium* spp.) was the only individually excavated root receiving substantial use during June as well as July and August. *Lomatium* was excavated on lithic, higher elevation ridges, whereas sweet cicely, yampa, and pondweed were dug at middle elevations in mesic forest, mesic nonforested areas, and seasonally inundated sites, respectively.

Volumes of flesh fruits showed a marked peak and constituted a substantial portion of total scats only during August. Whortleberry (*Vaccinium scoparium*), huckleberry (*Vaccinium globulare*), and soapberry (*Shepherdia canadensis*) formed the majority of fleshy fruits in the scats. A considerable number of leaves were typically ingested, with fruits of huckleberry and especially whortleberry; virtually all June use of whortleberry was of leaves.

Whitebark pine seeds composed a substantial portion of fecal volumes in May through October, with peak representation in September and October. Mean percent scat volumes were consistently among the highest recorded for any diet item. Whitebark pine seeds were acquired principally by extraction from cones dug out of red squirrel middens (Mattson and Jonkel 1990).

Human garbage and domestic livestock constituted a minor part of total feces, but received greatest use July through September; mean percent scat volume was especially high during August.

Mean scat diversity and variation

Diversity and among-years variation of mean scat contents varied appreciably among months (Fig. 1). Diversity increased from an all-year low in April to a peak in August and then to a secondary low in October. Among-years variation in scat content was highest in October but also high during May, August, and September. Variation was lowest in April.

Levels of feeding activity also varied considerably among months (Fig. 1). The number of scats collected per telemetry location visited (S_T) was low in April through June, and peaked during July and again during October. The proportion of telemetry locations without discernible signs of feeding was highest in April through June and consistently lower in July through October. These two measures were significantly and negatively correlated ($r = -0.866$, $P = 0.003$), and were interpreted as inverse measures of the same factor. The coefficient of among-years variation in S_T was substantially higher in May and October than in any other month.

We compared defecation rates per day of brown bears in European zoos (Röth 1980) with S_T values, by month. The range of values and pattern among months were remarkably similar (Fig. 1). Primary differences were that defecation rates peaked 1 month later than S_T values, and that a secondary S_T peak occurred in October. These differences had the characteristics of phase-shifted but otherwise similar patterns.

Individual-year scat contents

We observed major variations in scat contents among years,

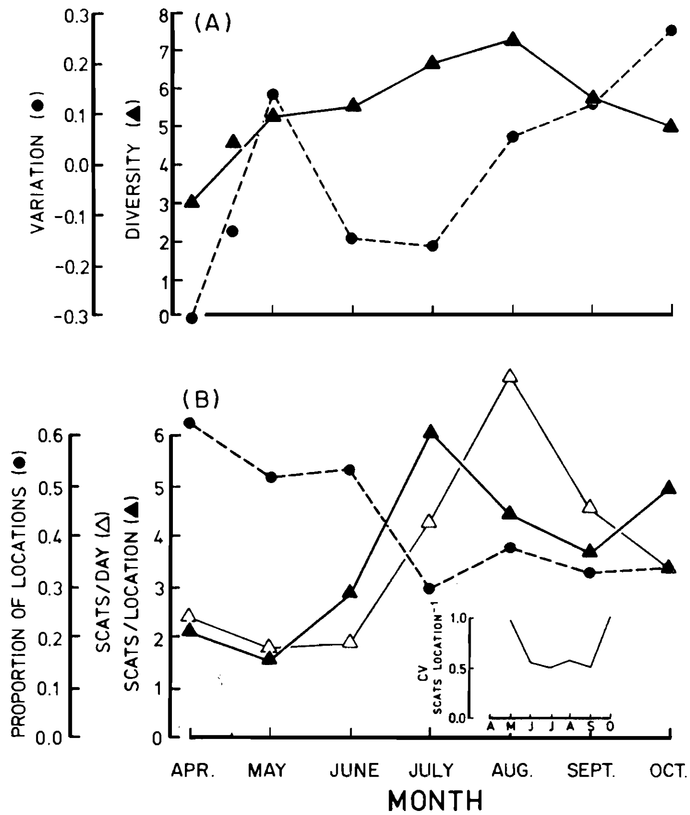

FIG. 1. (A) Index of among-years variation in mean content and diversity (e^H) of diet items in Yellowstone grizzly bear scats, by month. (B) Number of scats collected per telemetry location visited (S_T), number of scats produced per day by European brown bears in zoos (from Röth 1980), and proportion of grizzly bear telemetry locations visited at which no sign of feeding was found, by month. Inset shows the coefficient of among-years variation for S_T, by month.

and have so far not seen 2 years without significant differences (Fig. 2). Use of whitebark pine seeds varied substantially among years, from 1979, when this item composed most of the fecal matter in May through October, to 1977, when virtually no use was recorded. Use of pine seeds in May through July, which was especially evident during 1979, 1982, and 1986, reflected the availability of seeds overwintered from the previous fall (Mattson and Jonkel 1990). The 1978 crop was the largest ever observed, and the 1985 crop was the largest recorded on transects that we established in 1980 (Knight et al. 1988*b*).

Use of roots also varied considerably among years, especially during the fall. Large volumes of roots were defecated during the fall of 1977, 1982, and 1986, although species composition varied even among these years. Roots were mainly of pondweed and yampa during 1977, yampa during 1982, and sweet cicely during 1986.

Among-years use of graminoid and forb shoots was stable compared with that of pine seeds and roots. During virtually all years, large volumes of graminoids were found in May and June scats. Most variation in graminoid use occurred after June; in 1977, for example, there was a marked decline in graminoid use during July, and in 1983 and 1986 fecal volumes of graminoids were unusually large during September and October.

Additional features that distinguished certain years were the phenomenally large volumes of ants in the feces during July and August of 1977, the substantial use of army cutworm moths during July 1987, the high levels of ungulate use during the

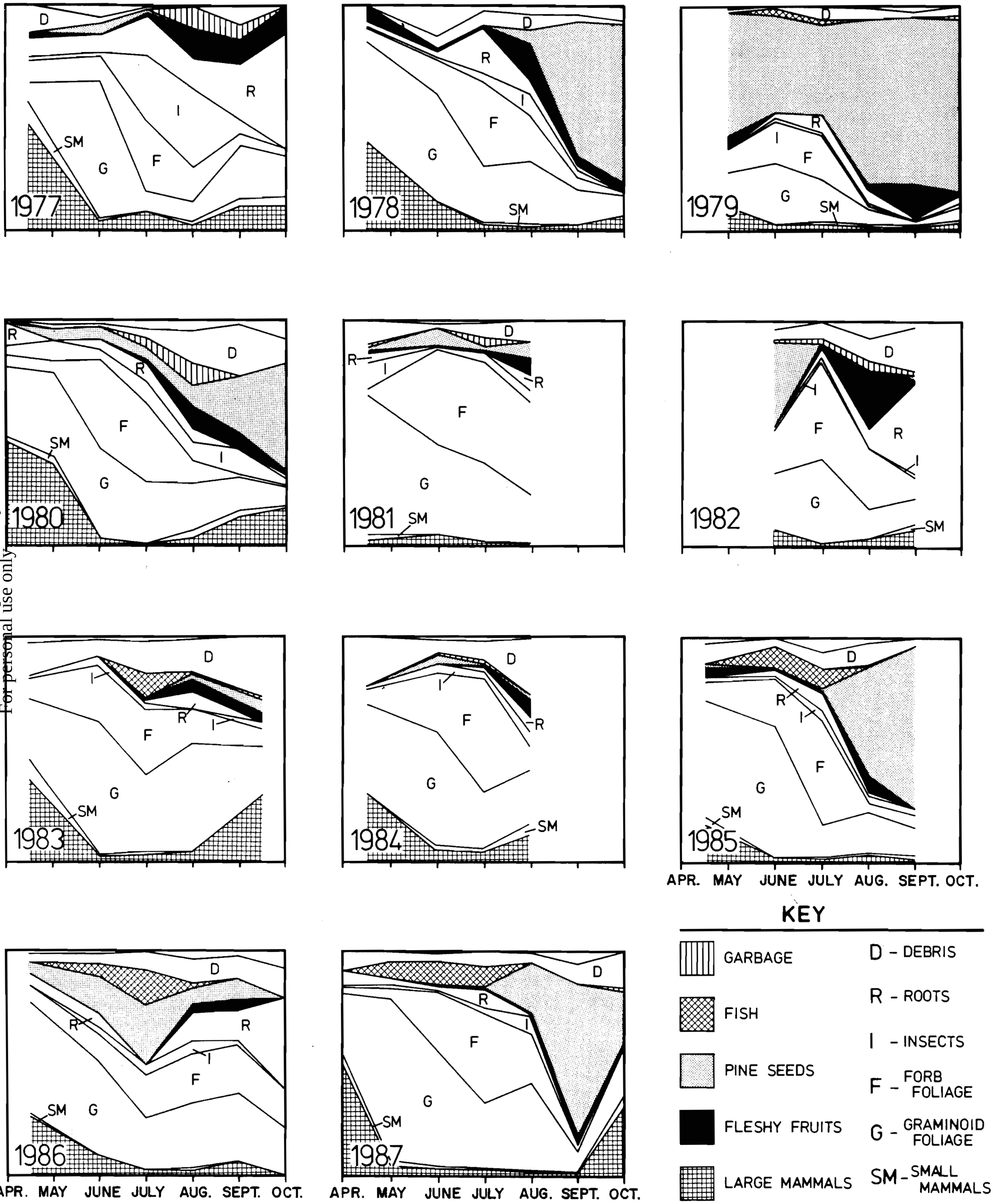

FIG. 2. Individual-year scat contents by month, 1977–1987. Width of band corresponds to proportion of diet items, summing to 1.00 (horsetail foliage was included under forb foliage).

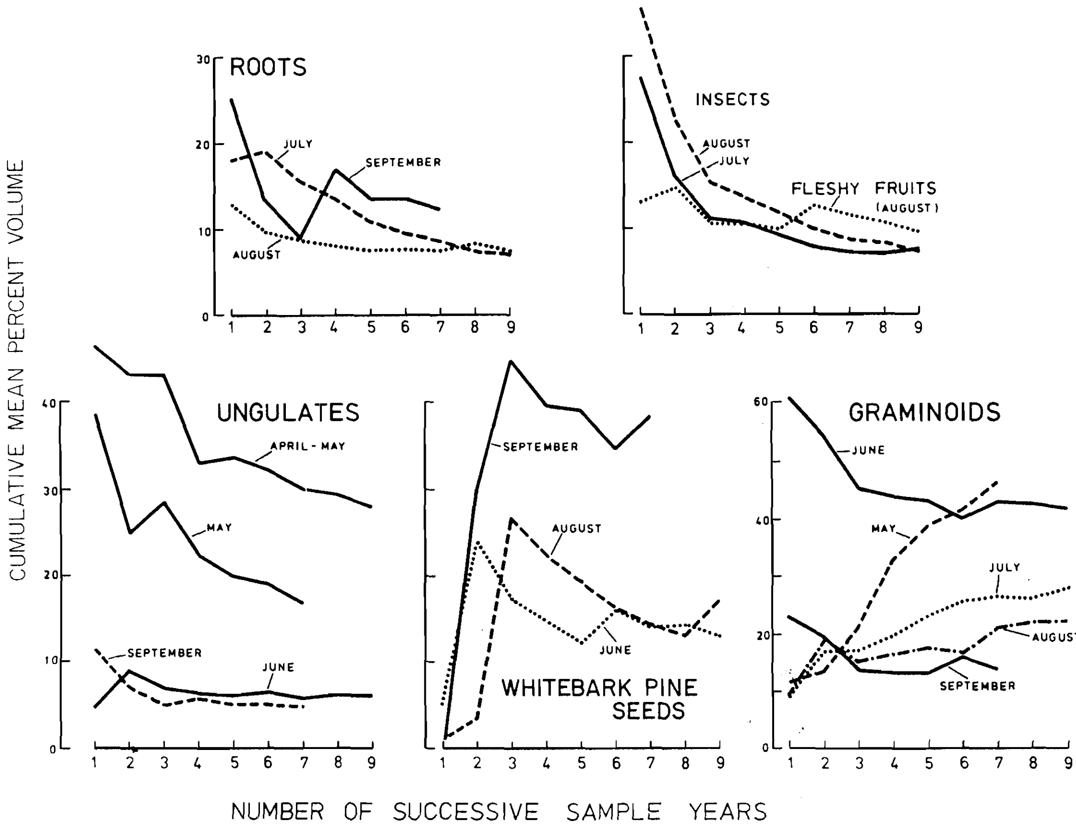

FIG. 3. Cumulative mean percent volumes of six diet items with increasing number of successive sample years; each year is given equal weight.

TABLE 2. Relative volumes of major diet items in scats in three food habit studies in the Yellowstone area

	Relative volume (%)		
Diet item	Murie 1944	Mealey 1975	This study
Mammals	2.1	8.4	8.3
Cutthroat trout	0	5.4	1.0
Insects	3.3	1.0	5.8
Graminoids	49.7	35.7	23.8
Forbs (stem)	25.8	33.0	22.8
Roots	5.7	3.3	4.3
Fleshy fruits	5.7	3.3	4.3
Whitebark pine seeds	0.4	2.8	25.7
Other foods	11.6	2.3	3.2
No. of years	1	2	7
No. of scats	243	615	2569

NOTE: Volumes were rescaled to exclude debris, and so that the seasonal sampling regime of this study corresponded to that in Mealey (1975).

spring of 1977, 1978, and 1980, the remarkably early (August) use of the current year's pine seed crop during 1987, and the unusually large volumes of fleshy fruits in scats during August 1982.

Mean percent volumes in scats in relation to number of sample years

We plotted cumulative mean percent volumes for major diet items against the number of sequential sampling years (Fig. 3). This provided a means of evaluating the relationship between number of years of data collection and stabilization of the estimates of percent volume.

For most months and diet items, estimates stabilized with 4–6 years of data. However, after inclusion of 7 years' data, the September estimates of percent pine seed volume still varied widely. Perhaps most significantly, relative volumes of ungulates in April and May, graminoids in May, roots in July, and insects in August showed long-term trends that had not substantially moderated even after 7–9 years of sampling. Our analysis suggested the existence of endemic variation, most of which had dampened after 4–6 years. Superimposed on this was longer term variation, manifested in trends spanning at least a decade.

Comparison of studies carried out in the Yellowstone area

We compared our results with estimates of mean percent scat contents from data collected by Murie (1944) and Mealey (1975) (Table 2). We rescaled the results from our 7 consecutive years of data so that the seasonal sampling regime corresponded to that of Mealey (1975). We also rescaled the results from the three studies to exclude debris. The results of all these studies were obtained in approximately the same study area but relied on substantially different sample sizes, in terms of both years and scats.

There were major differences in the estimates from the three studies. The single largest difference was the many fewer pine seeds in scats collected by Mealey and Murie. We also documented appreciably larger volumes of insects and smaller volumes of trout than did Mealey. Larger volumes of forbs, especially graminoids, in the earlier studies complemented their small pine seed volumes.

Discussion

Among-years variation

Our results point to the pitfalls of viewing bear diets in an average sense or on the basis of only a few years' data. Grizzly bears in our study area engaged in large-scale year-to-year diet switching. Even after 11 years of data collection, new and significant dietary patterns and use of diet items were still evident. We detected substantial use of some items during only 1 of the 11 study years. These items were presumably of great significance to the bear population during the infrequent years of heavy use; they included ants during summer 1977, pondweed during spring and fall 1977, and sweet cicely during 1986. It took us 9 years to detect highly concentrated and, according to all the evidence, ongoing use by bears of army cutworm moths on high alpine talus. Superimposed on this endemic variation is the possibility that long-term trends in bears' food habits in the Yellowstone area have been influenced by climatic fluctuations and changes in management of fish and ungulate populations (Picton et al. 1986; Green and Mattson 1988; Reinhart and Mattson 1990).

For a marginally viable population, for which mortality risk is affected by annual variation in food availability, documentation of trends and episodically significant periods of food is essential to management, and to understanding population regulation. If we had relied on 2 years' data collected early in our study, we might have completely failed to appreciate the importance of whitebark pine seeds in the diet of the Yellowstone grizzly bears. Much of the documented bear mortality and management actions in the Yellowstone area has varied inversely with availability of pine seeds (Picton et al. 1986; Knight et al. 1988*a*). In habitat as potentially varied as our study area, adequate documentation of bears' food habits for management purposes will probably necessitate a long study, spanning at least 4 and possibly as many as 10 years.

Large-scale variation in diet among years as well as months suggests that Yellowstone grizzly bears were sampling a spectrum of foods, many of which may have been present as undetected trace amounts in collected scats. It is otherwise hard to explain why the bears started widespread and intensive use of sweet cicely roots during 1986, when use of this food had not been conclusively documented from scats or at feeding sites any of the previous 9 years. Benefits undoubtedly accrue to bears from ongoing sampling of potential foods, given the probability of major changes in quantity or quality of both heavily used and as yet unexploited foods.

Defecation and ingestion rates

Our results suggest that the number of scats collected per telemetry location visited (S_T) could provide an index of defecation and ingestion rates for bears. By itself, S_T could reflect defecation rates, scat collection efficiencies, or scat detectabilities. However, because S_T corresponded to defecation of bears in zoos, which are fed constant-composition diets, and was negatively correlated with detection of feeding activity, we concluded that this measure largely reflected the defecation rates of bears in our study area. If S_T is further validated, and is applicable elsewhere, then comparisons of defecation–ingestion rates among time periods or similar study areas may be possible using field data.

S_T values suggested that Yellowstone grizzly bears ingested relatively little in April through June, and ingested the greatest volumes in July, August, and October. The early-season low value coincided with estrus and breeding (Craighead et al. 1969; Craighead and Mitchell 1982; Schleyer 1983) and post-den-emergence hypophagia (Nelson et al. 1983; Nelson et al. 1984), physiological and behavioral phenomena that logically correspond to low feeding rates. We interpreted the high late-season rates as evidence of hyperphagia (Nelson et al. 1983), starting as early as July in the Yellowstone area. The high variability in S_T during May and October suggests that feeding levels and the significance of foods during these months varied substantially among years, and that bears were probably responding to the availability of high-quality foods during May and October and sufficiency of foods in July through September.

Seasonal variation

Variation in scat composition among months, like that among years, suggested large-scale seasonal diet switching by Yellowstone bears, almost certainly to conform to the availability of high-quality foods, and in response to digestive and nutrient constraints (cf. Stirling and McEwan 1975; Herrero 1978; Bacon and Burghardt 1983; Hamer and Herrero 1987). Of high-quality foods, use of whitebark pine seeds was contingent on their maturation in August (cf. Hutchins and Lanner 1982) and the size of the overwintering crop (Mattson and Jonkel 1990). When available, the high-fat-content pine seeds (Mealey 1980) were used to the near exclusion of other foods, no doubt because of their high energy content and contribution to body fat accumulation (Hadley 1985; Brody and Pelton 1988). Most fleshy fruits ripened by early August, but their use in the Yellowstone area was restricted by chronically poor production, limited acreage of productive plants, and low efficiencies associated with use of the widespread but small-fruited whortleberry (Craighead et al. 1982). Ungulates were used when they were most vulnerable, as winter-killed or weakened animals during spring (Green and Mattson 1988; Henry and Mattson 1988), calves during May and early June (Gunther and Renkin 1990), or weakened bulls during the fall rut (Schleyer 1983). Use of trout was closely tied to June and July spawning runs around Yellowstone Lake and was the predominant feeding activity by a number of bears during that time in that area (Reinhart and Mattson 1990; Reinhart 1990).

Use of lower quality foods also reflected seasonal variation in quality and quantity, but was also apparently contingent on availability of higher quality foods. Peak May and June use of graminoids reflected unavailability of new year's growth during April and a typical decline in quality during July (cf. Skolvin 1967; Pond and Smith 1971; Graham 1978). Use of forbs and ants was mostly obscurely related to their quality and abundance, and implied their status as back-up or secondary foods, although the July peak in forb use probably reflected a general tendency of forb foliage to be of higher quality than graminoids later in the growing season (Cook 1972; Thomson 1984). We hypothesize that secondary compounds also probably played a significant role in determining bears' use of forbs in the Yellowstone area (cf. Freeland and Janzen 1974; Robbins et al. 1987).

Monthly differences in scat content diversity and among-years variation offered insight into the way Yellowstone grizzly bears responded to their foraging environment. The high year-to-year stability and low diversity of April's diet suggested consistent but few foraging options, primarily ungulates and precocious graminoids. Although we did not have enough years of data to address variation in S_T during April, high among-years variation in S_T during May was suggestive of a similar situation during April and high variation in ingested volumes.

The greater diversity and high among-years variation in May scat composition reflected the season advent of more foraging options. During some years abundant carrion was still available, during warmer years graminoids had grown enough to be a major food, and during years following a large crop, pine seeds were dug from middens under the snowpack. Bears apparently responded to these varied opportunities by large-scale adjustments of their diet and ingestion rates, probably mediated through metabolic states. Bears cannot ingest a high-protein-content diet such as ungulate carrion and maintain hibernation metabolism (Nelson et al. 1975; Nelson 1980), which would represent an effective means of conserving energy during a May, when few high-quality foods are available, and would result in lower defecation rates (cf. Nelson et al. 1983).

During most years, June foraging was probably dictated more by reproductive and security requirements than distribution of foods (Stroganov 1962; p. 130; Pearson 1975; Herrero and Hamer 1977; Craighead and Mitchell 1982). Low-intensity and relatively invariant primary use of the abundant grazing resource during June as well as May consequently represented a relatively minor part of the overall diet, and very likely contributed little to the condition of most bears. The May through July weight loss of most bears in the Yellowstone area (Blanchard 1987) was probably as much a consequence of low-volume ingestion as of low diet quality.

The combination of high defecation rates, high scat content diversity, and low among-years diet variation during July probably resulted from the relatively consistent availability of moderate-quality foods and the related greater tendency of individual bears to specialize (cf. Hughes 1979). We routinely observed individual bears during July exclusively and concurrently feeding on a variety of moderate-quality foods; for example, one bear dug biscuitroot on high ridges, while another dug yampa in the valley below and another grazed clover. With consistent food availability and high diet variation among bears, high average diet diversity would be consistent with hyperphagia and high among-years diet stability. During August this scenario tended to break down, with the advent of higher quality foods such as fleshy fruits and pine seeds; this apparently resulted in greater similarity of diet composition among bears.

During September and October high-quality foods were not consistently available, and the quality of the grazing resource further declined. Predictably, this resulted in greater among-years diet variation and lower average diet diversity. As during May, the greater among-years variation in diet composition and inferred defecation rates during October may have reflected variable onset of hibernation metabolism and cessation of foraging.

Comparisons among studies

The average Yellowstone grizzly bear's diet was distinguished by ingestion of large volumes of ungulates, graminoids, and pine seeds during spring, summer, and fall, respectively, and correspondingly low volumes of fleshy fruits. Within North America, this diet was most similar to that of grizzly bears in drier portions of Montana (Craighead et al. 1982; Aune and Kasworm 1989) and differed from those of virtually all other bear populations by the paucity of fleshy fruits. Only three other brown bear populations in North America ate as few fleshy fruits (Reynolds 1981; Craighead et al 1982; Nagy et al. 1982); these populations were at either high elevations or high latitudes. Also, with the exception of a few arctic brown bear populations (Nagy et al. 1983; Reynolds and Garner 1987), brown bears in North America did not make as much use of ungulates as did grizzlies in Yellowstone.

A comparison of the diets of bears outside North America showed that the diet of Yellowstone's grizzlies was remarkably similar to that reported for brown bears in central Siberia (Stroganov 1962; Ustinov 1965), where ungulates and seeds of stone pines (*Pinus sibirica* and *P. pumila*) were important high-quality foods, and fleshy fruits were little used. Otherwise, like most North American brown bears, Eurasian brown bears relied on fleshy fruits and, in coastal areas, spawning salmonids for fattening.

Fleshy fruits are greatly preferred by black bears (Bacon and Burghardt 1983), and their major role in virtually all brown bear diets in areas where brown bear populations attain at least moderate densities suggests a positive relationship, although the availability of ungulates can likewise influence brown bear population densities (Kaal 1976; Filonov 1980; Reynolds and Garner 1987). It may be significant that bears will abandon spawning salmon to consume fleshy fruits as they become available (Bergman 1936; Clark 1956; Bromlei 1965, Berns and Hensel 1972), conceivably because, relative to proteinaceous foods, foods containing a large portion of digestible carbohydrate are more efficiently converted to fat (McDonald et al. 1981) and so would expedite fat accumulation during hyperphagia.

In most areas, brown bears eat large volumes of fleshy fruits during most of the period of hyperphagia, from late July or early August through September. In areas such as Yellowstone, where bears rely on pine seeds, the seeds are available for a shorter time, typically beginning in late August. Consequently, relatively little high-quality food is available during part of the period of hyperphagia, July and early August. Pine seeds are also an unreliable foods source (Knight et al. 1988*b*; Craighead et al. 1982), and there are many years during which Yellowstone grizzlies rely instead on roots or foliage for fattening. Conversely, in most temperate areas where bears subsist on fleshy fruits, a variety of berry-producing shrubs provide alternative higher quality food when the primary fruit crop fails. As is the case in the Yellowstone area, where a single shrub species produce virtually all the usable fleshy fruits, in Banff and Jasper National Parks (Russell et al. 1979; Hamer and Herrero 1987) and the Yukon (Pearson 1975), bears also rely more on roots for subsistance during poor berry years, and population densities are apparently low.

Prior to 1970, grizzly bears had free access to human refuse during July and August in Yellowstone Park Craighead and Craighead 1971). This early-season use of garbage probably explains the higher body weights of bears in the 1960s, when garbage was readily available in the Yellowstone area, and the lower weights in the 1970s and 1980s, when it was not (Blanchard 1987). Consumption of garbage during the 1970s also probably explains the differences in productivity and weight among females who used the few remaining dumps and those that did not (Blanchard 1987). Garbage was probably not a higher quality food than fleshy fruits and pine seeds, but its availability during the early part of hyperphagia was probably significant for bears in Yellowstone area.

Feeding on garbage did not influence the nutritional well-being of most bears subsequent to 1973, and garbage was of greater significance as an attractant that brought bears into conflict with humans (Knight et al. 1988*a*). Even though Yellowstone-area grizzlies are known to use domestic livestock (cf. Jorgenson 1983; Knight and Judd 1983) and garbage (Knight et al. 1988*a*), these items composed a small part of the average diet. Other human-introduced and less closely associated foods such as *Poa pratensis, Trifolium repens*, and *Taraxacum officinale* composed a greater part of grizzly scats and where nutritionally significant to the population.

For the reasons addressed above, we hypothesize that the density of grizzly bears in the Yellowstone area is limited in large measure by the lack of fleshy fruits, though this was mitigated by the availability of edible human refuse during the three decades prior to 1970. Irregularity of pine seed production is probably the next most limiting habitat factor, primarily because during years when pine seed production is low, grizzly bears come into greater conflict with humans (Knight et al. 1988*b*) and more bears are killed (Knight et al. 1988*a*).

Bias and error

We concluded that our scat sample was not appreciably affected by biases otherwise associated with scat collection along recreational trails and subjectively selected routs. Approximately 30% of our scats were collected at locations of radio-collared bears, and virtually all our backcountry travel concentrated on these telemetry locations. Consequently, most scats not collected at telemetry locations were found along natural travel routes such as game trails and ridge crests rather than along recreational trails.

Obtaining adequate sample sizes is conceivably a major problem for bear food habits studies using scats (Lloyd 1979). Given typical among-scats variation in composition and reasonable confidence intervals, required sample sizes are in the neighbourhood of 300–1000 scats (cf. Hanson and Graybill 1956; Zar 1984, p. 108). We achieved this sample size for our entire sample and for a few months. However, the information conveyed by averages over all months and years and even over all years for a given month was of limited interest, and was useful primarily for comparisons among study areas. Documentation of among-years and among-months variation was critical to our understanding of bear foraging strategies and habitat relationships, and underpins effective management. Whatever deficiencies may be attributed to our sample sizes, these samples were larger over a longer period of time than those of any other reported study. Our estimates of average scat contents likely provide an accurate picture of grizzly bear fecal matter in 1977–1987, and our individual-year diagrams likely depict scat contents sufficiently for among-years comparisons to be made.

Black bear scats almost certainly constituted a percentage of our sample. We had no cost-effective and reliable criteria for distinguishing between black bear and grizzly bear scats (cf. Hamer et al. 1981) other than by association with tracks or sightings. However, the percentage of black bear scats collected was probably low. Our sampling effort focused on radio-collared grizzlies and was often in areas where there were known to be few black bears. Analysis of hair samples taken from 100 bear beds during habitat sampling (93% of total beds sampled during 1979)[1] corroborated the probably minor contribution of black bears to our fecal sample. Seventy percent of all hair samples were from grizzly bears and only 17% from black bears. Remaining hair samples were from other mammals.

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