THE NATURAL FOOD HABITS OF GRIZZLY BEARS IN YELLOWSTONE NATIONAL PARK, 1973-74[1]

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Abstract: The natural food habits of grizzly bears (*Ursus arctos horribilis* Ord) in Yellowstone National Park were investigated in 1973-74 to identify the grizzly's energy sources and trophic level(s), nutrient use, and distribution. Food consumption was determined by scat analysis and field observations. Food quality and digestibility were estimated by chemical analysis. Grizzlies were distributed in 3 distinctive feeding economies: *valley/plateau*, a grass/rodent economy where grizzlies were intensive diggers; *mountain*, primarily a grass/springbeauty/root economy where grizzlies were casual diggers; and *lake*, primarily a fish/grass economy where grizzlies were fishers. The economies occured in areas with fertile soils; distribution of bears within each was related to the occurrence of succulent plants. The feeding cycle in the valley/plateau and mountain economies followed plant phenology. Grizzlies fed primarily on meat before green-up and on succulent herbs afterwards; meat, corms, berries, and nuts became important during the postgrowing season. Succulent grasses and sedges with an importance value percentage of 78.5 were the most important food items consumed. Protein from animal tissue was more digestible than protein from plant tissue. Storage fats were more digestible than structural fats. Food energy and digestibility were directly related. Five principle nutrient materials (listed with their percentage digestibilities) contributed to total energy intake: protein from succulent herbs, 42.8; protein and fat from animal material, 78.1; fat and protein from pine nuts, 73.6; starch, 78.8; and sugar from berries and fruits, digestibility undetermined. Protein from succulent herbs, with a nutritive value percentage of 77.3, was the grizzlies' primary energy source. Because succulent, preflowering herbs had higher protein levels than dry, mature herbs, grizzly use of succulent herbs guaranteed them the highest source of herbaceous protein. Low protein digestibility of succulent herbs was compenstated for by high intake. Grizzlies were digestively flexible and maximized use of protein from plant and animal sources. They were adapted to the most constant and abundant sources of protein: succulent herbs and animal material from open, fertile grasslands. Competition among grizzlies for animal food during the pregrowing season may be regulatory for the grizzly population. The grizzly population level can be partially accounted for by the grizzlies' status as secondary consumers during pregreen-up periods and primary consumers during the growing and postgrowing seasons. The essential environmental requirement was the availability of fertile grasslands and herblands interspersed with cover and capable of maintaining artiodactyls, rodents, and abundant nutritious herbs as sources of food.

Extensive grizzly bear (Rausch 1963) use of unnatural foods (garbage and camp groceries) in Yellowstone National Park occured from the early days of the park until closure of the Trout Creek and West Yellowstone open-pit garbage dumps in 1971 (Skinner 1925, Cole 1976). After these primary sources of unnatural foods were removed, most grizzlies resumed use of natural foods (Cole 1974).

This report on grizzly bear use of natural foods is based on research conducted in 1973 and 1974 as part of the Interagency Grizzly Bear Team Study. The overall objectives were to develop hypotheses about the grizzly's natural energy sources and tropic level(s), the quality and quantity of nutrient use, and grizzly distribution.

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STUDY AREA

The study area included all of Yellowstone National Park, which occupies about 8,900 km^2 in the states of Wyoming, Montana, and Idaho. The geology of the park was described by Keefer (1972) and Eaton et al. (1975), the climate by Lowery (1959), and the vegetation zones by Despain (1973b). Soil types in the park were described by Washington (1917), Despain (1973a), and Stermitz et al. (1974).

Interactions among the park's geologic events, climate, soils, and vegetation resulted in 3 apparent physiographic/vegetative units (Fig. 1). These units are as follows: (1) the mountainous unit with the spruce-fir (*Picea engelmanii-Abies lasiocarpa*) and alpine-tundra zones and herblands and grasslands covering fertile andesitic soil; (2) the valley and plateau units with grasslands and the Douglas-fir (*Pseudotsuga menziesii*) zone covering fertile, transported soils; and (3) the plateau unit with lodgepole pine (*Pinus contorta*) covering infertile rhyolitic soils.

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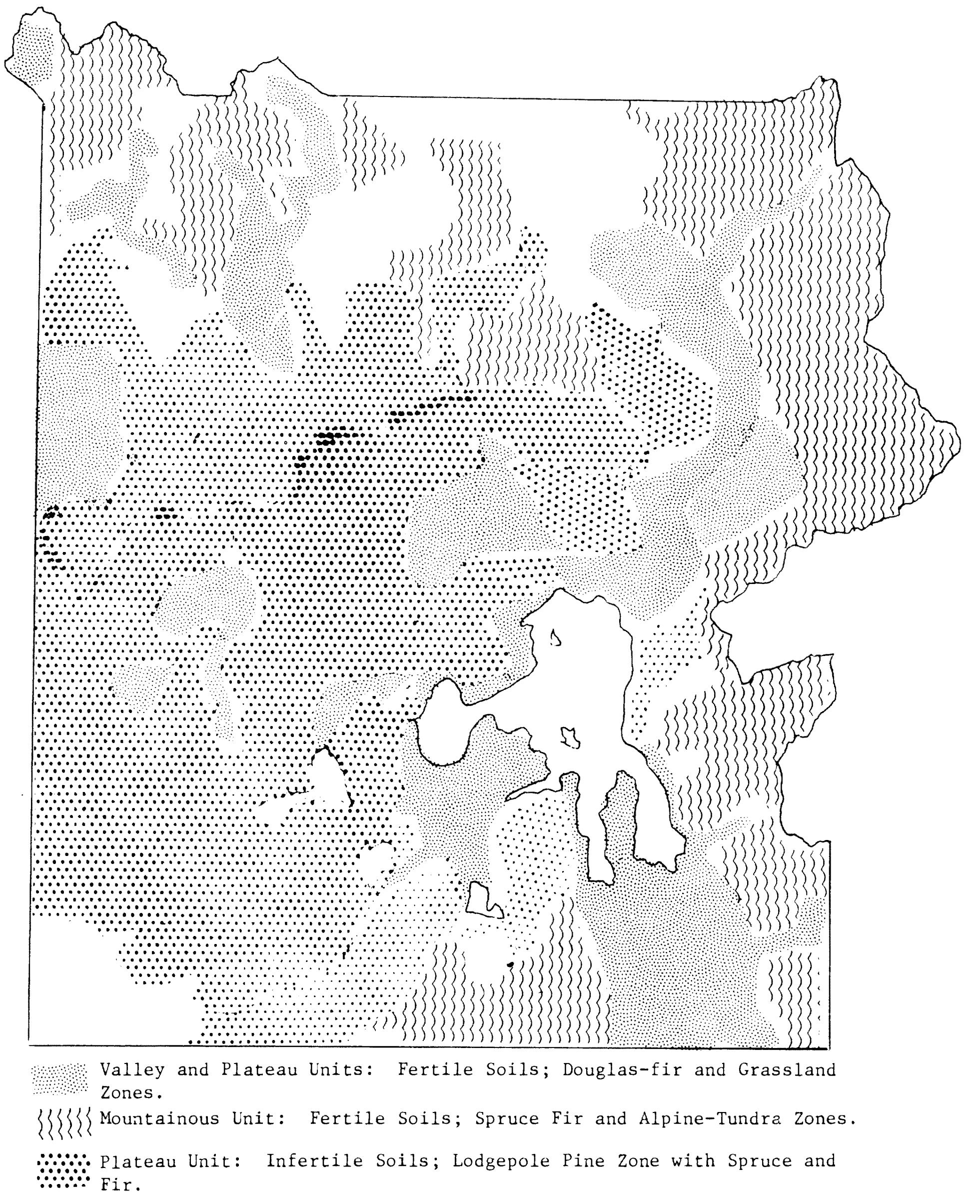

Fig. 1. Map showing 3 generalized physiographic/vegetative units in Yellowstone National Park.

METHODS

Quantitative Analysis: Scat Collection, Preparation, and Analysis

Collections of scats and visual obeservations of feeding that were made during 557 man-days in the field were used to determine the quantitative importance of food items used by grizzly bears. In 1973, this activity was parkwide, excluding the Absaroka Range. In 1974, activity was concentrated in major use areas identified in 1973.

Size distinguished grizzly scats from black bear scats; those with diameters 5 cm or greater were normally considered grizzly scats (Murie 1954). Several field observations verified the validity of this criterion. Other evidence considered in identifying grizzly scats consisted of associated track sign and feeding activity sign, visual observation of bears, and the general nature of the location. Scats with diameters less than 5 cm were assumed to be those of small or immature grizzlies only if there was some evidence of grizzly use of the location.

Every grizzly scat located singly was collected. When groups of 10-25 scats were located, one-half the total in each group was collected. When groups of more than 25 scats were located, one-third the total in each was collected. All scats were individually identified according to location, altitude, vegetative surroundings, and age estimated to the nearest month by characteristics of the site (Mealey 1975). Scats were air-dried for storage; those that were extremely moist or infested with insect eggs or larvae were oven-dried at low heat to kill organisms that could change the nature of scat contents.

Analysis of scat contents was conducted in the field and in the laboratory. Scat contents were more identifiable when fresh in the field, and plant remains were easily compared with nearby specimens. Materials analyzed in the field were taken to the laboratory for further study.

Analysis of bear scats in the laboratory followed the techniques of Tisch (1961). Russell (1971), and Sumner and Craighead (1973). Basic steps involved (1) rehydration of fecal material to render it pliable and to restore its original form, (2) separation of material into homogeneous groups by use of screens (No. 10 and No. 20 mesh), (3) identification of contents, and (4) recording of identified materials.

Identification to species, through macroscopic and microscopic examination, was usually successful for all plants except grass and sedge. Animal materials were identified with the aid of reference collections of bones and hair and textual references (Spence 1963, Hoffman and Pattie 1968).

The occurence and volume of each identified food item were recorded as each scat was analyzed. Visual estimates of volume were recorded under 1 of 4 categories: trace-25 percent, 25-50 percent, 50-75 percent, and 75-100 percent. Estimation of scat composition by volume undervalued the use of some foods as indicated by proximate analysis techniques that established differential digestibility of food items.

Data were grouped in a number of categories including 3 that related grizzly food use and plant phenology: pregrowing season, 1 April-1 June; growing season, 1 June-1 September; and postgrowing season, 1 September-15 November. These periods reflect plant growth conditions in Yellowstone Park (D. G. Despain, personal communication, 1974).

Food items were ranked according to importance value (Sumner and Craighead 1973) calculated as:

$$\text{Importance value} = \frac{\text{Percent frequency of occurrence} \times \text{Percent of diet volume}}{100}$$

where percent frequency of occurrence equals the total number of times a specific food item appeared in scats of the sample group, divided by the total number of scats in the sample; and percent of diet volume equals the total percentage volume of an item occurring in scats of the sample group, divided by the total number of scats in the sample.

Importance value was chosen as the indicator of food item importance because it establishes relative equilibrium between items that occurred frequently but in low volume percentages.

Percents composition per item and importance value percents were calculated. Percentage composition per item suggests a degree of selection for particular foods; values were derived by dividing the total percent volume of an item by the total number of scats containing that food item. Importance value percentages were derived by adding the importance values in the group and dividing individual values in the group by the sum.

Qualitative Analysis: Food Quality, Digestibility, and Nutritive Value

Identities, energy values, and apparent digestibilities of the principal nutrient materials of the most important grizzly foods were determined, as were seasonal nutritive values.

Standard proximate analysis procedure detailed by Crampton and Harris (1969) was used in estimating the quality and apparent digestibility of food items. Food items containing starch were also evaluated by a special starch analysis method (Banks et al. 1970). Food quality is defined in terms of the amounts of protein, fat, and carbohydrate present in a food item and the caloric values of the item. Apparent digestibility is an estimate of nutrient utilization and digestive efficiency. Digestibility was estimated by calculating the percentage of nutrient intake not present in food item residues in scats.

Determinations of food quality and apparent digestibility were subject to a minimum of 4 sources of possible error: (1) analytic procedures could not account for all material completely assimilated; (2) in proximate analysis, nitrogen-free extract values are determined by difference; (3) feces probably contained protein and fat from nondietary origin (Crampton and Harris 1969); and (4) sampling error.

Food items and scats containing residues of the same items were collected at the feeding sites. Scat and food item samples were paired and submitted for analysis. Analytical methods for proximate analysis followed the Association of Official Agricultural Chemists handbook (Horowitz 1975), and the analyses were performed by the Analytical Chemistry Laboratory of Montana State University.

The digestibilities of 4 principal grizzly nutrient materials were estimated by averaging the values for individual food items.

Seasonal nutritive values were calculated from data on seasonal food use in 1974. Nutrient importance values were determined by a method similar to that used for the determination of food item importance values.

A nutritive value index (NVI) of the principal nutrients was calculated to estimate each nutrient's contribution toward the grizzly's energy intake. The index was calculated according to the formula:

$$\text{NVI} = \frac{\dfrac{\text{Nutrient intake percent}}{\text{(Percent importance value)}} \times \dfrac{\text{Digestibility}}{\text{percent}}}{100}$$

Nutritive value indices were converted to percentages to facilitate comparisons.

RESULTS

Distribution

Grizzly distribution in the park was influenced by unique processes of interaction between bears and their foods. In 1973, 3 such processes were hypothesized and each identified as an economy. These were the *valley/plateau, mountain,* and *lake* economies. The basis for initially distinguishing these economies was the simultaneous occurence of scats in each. After further study in 1974, each economy seemed to represent a mix of physiographic and biotic conditions resulting in a characteristic pattern of interactions between grizzlies and food items that allowed the bears to maximize food use. Each economy appeared to represent a center of concentrated grizzly feeding activity determined by locations of scats collected in 1973 and 1974. Areas of high grizzly density determined by aerial surveys were coincident (Knight 1974, 1975).

Feeding economies were centered on areas with fertile soils (Fig. 1). Little feeding activity was apparent on infertile soils. Highest grizzly densities, excluding the lake economy, were reported on the rich grasslands of Hayden and Pelican valleys (Knight 1975), although use of these areas was not as evident in 1975 as in 1973-74 (Knight 1976).

Valley/Plateau Economy

Major epicenters of the valley/plateau economy were Hayden, Pelican, and Lamar valleys, and Cougar Creek Flat. Fertile, transported soils support an abundant grassland biota that provided most of the food used in the economy. The valleys and flat were largely surrounded by plateaus with infertile soils and lodgepole pine forests. The plateau component provided cover and occasional food.

Comparing grizzly foods of the valley/plateau economy between years indicated that the diets in 1973 and 1974 were similar. Grasses and sedges were the most important items both years. The importance of white clover (*Trifolium repens*) and elk thistle (*Cirsium foliosum*) differed between years because an area with scats containing primarily the remains of these items was sampled in 1973 but not in 1974. For the 2-year period, grasses and sedges constituted 82 percent of diet importance.

The general feeding cycle appeared to follow plant phenology. During the pregrowing season, grizzlies were primarily meat eaters, congregating on ruminant wintering areas and taking the animal material available. Cole (1972) has detailed this activity. Corms, roots, and grass were eaten before and during early green-up. During the growing season, grasses, sedges, forbs, and rodents were the primary foods. Succulent vegetation in open areas near cover was perferred; its availability, linked with that of rodents, influenced distribution of grizzlies. Most plants were succulent at that time and bears were widely distributed.

During the postgrowing season, succulent grasses and forbs remained important foods. Since these foods were associated only with moist sites, feeding was limited to such sites and bears were narrowly distributed. Seasonal foods in the lodgepole pine forests became available as grasses, sedges, and forbs in the valleys desiccated; whitebark pine (*Pinus albicaulis*) nuts, and berries were taken along with mushrooms (*Russula* sp.) and the rhizomes of smilacina (*Smilacina* sp.). Predation on male, breeding elk (*Cervus canadenis nelsoni*) may also have occurred. Extensive use was made of melica (*Melica spectabilis*) corms in Pelican and Lamar valleys.

Intensive digging was the characteristic feeding activity of grizzlies in the valley/plateau economy, especially during the growing season. Pocket gophers (*Thomomys talpoides*) and voles (*Microtus* sp.) apparently motivated this activity. Locally concentrated excavations ranged in volume from a few hundred cubic centimeters to nearly a hundred cubic meters. Most were from 1 to 5 m^3 in volume. Large numbers of scats were often found at digging sites. Average residues in scat contents were 90 percent grasses and forbs and 10 percent rodents. Grizzlies apparently pursued rodents but often settled for grasses, forbs, and a small amount of meat. Bears were observed locating, digging out, and eating roots, corms, bulbs, and young gophers. The small but consistent degree of success in catching rodents probably held the bears in the feeding pattern. Intensive digging activity and associated evidence of grazing usually occurred in locations where xeric sites were interspersed with mesic or hydric sites. The excavations occurred on the xeric sites and grazing occurred on the adjacent mesic or hydric sites.

White clover was used extensively where it was abundant and associated with other foods. As many as 50 scats containing only white clover residues were found in individual white clover patches.

Possession of a bull elk carcass during the postgrowing season, after herbs had dried, did not preclude a grizzly's other foraging activities. Most scats collected near its meat cache contained residues of plants and elk.

Mountain Economy

The Gallatin and Washburn ranges were major centers of the mountain economy. Their fertile andesitic and sedimentary soils supported abundant vegetation in mountain meadows, herblands, parklands, and on ridgetops.

The most important food items consumed in the mountain economy in 1973 and 1974 were identical and were similarly ranked. For the 2-year period, springbeauty (*Claytonia lanceolata*) ranked first in food consumption importance, grasses and sedges ranked second, the roots of Umbelliferae ranked third and whitebark pine nuts ranked fourth.

Again, the general feeding cycle followed plant phenology. There were elk and moose (*Alces alces shirasi*) wintering areas in the economy, and use of ruminant material probably occurred during the pregrowing season although this period was not sampled. During the growing season, springbeauty, grasses, and sedges were the most important foods. Springbeauty was taken primarily in ridgetop herblands; grasses and sedges were taken in meadows and parklands. Feeding activities and distribution of bears in relation to these foods were influenced by plant succulence. Feeding began in snow-free locations and followed snowmelt and green-up to the highest elevations by late June and August. After desiccation of plants on the highest ridgetops in late August, feeding occurred at lower elevations where plants remained green. Such sites were stream bottoms, springs, and herblands associated with persistent snowbanks. During the early postgrowing season, feeding activities continued to be influenced primarily by succulent vegetation on moist sites. Pine nuts and gooseberries (*Ribes setosum*) appeared to be incidental foods. In October, after the desiccation of most herbs, feeding activity was concentrated on ridges at elevations of about 2,740 m where pine nuts, Umbelliferae roots, and springbeauty corms were taken exclusively.

Foraging patterns of the early postgrowing season in the mountain and valley/plateau economies were similar in that grizzlies concentrated on moist sites with succulent herbs and used seasonal foods incidentally. Foraging in the late postgrowing season was different in the 2 economies because grizzlies in the mountain economy ate pine nuts, roots, and corms on high ridges, whereas in the valley/plateau economy grizzlies fed on grasses, forbs, pine nuts, mushroons, rhizomes, and ruminants in the lodgepole pine forest.

Casual digging for springbeauty corms and biscuitroot (*Lomatium cous*) roots was the characteristic feeding activity of grizzlies in the mountain economy. The resulting excavations were usually shallow, a few cubic centimeters in volume.

Eating of whitebark pine nuts occurred in 2 ways. Incidental use occurred in late August and September, when the mature cones remained on the trees. Since most grizzlies do not climb, the only cones available to the bears during this time were those on the ground as a result of squirrel (*Tamiasciurus hudsonicus*) cuts and windthrow. Exclusive use occurred in October and probably November after cone disintegration and/or abscission. At that time, nuts and cones were abundant on the ground and grizzlies were linked directly to them. A move to higher-elevation ridges where whitebark pine is abundant was a response to cone disintegration and abscission.

Grazing on grasses and sedges was concentrated in dense stands of succulent forage at least 8 cm tall. Grizzlies usually grazed with a sideways motion of the head, which placed the muzzle perpendicular to the vegetation. The food was grasped with the molars and plucked. Feeding activity was rapid and was sustained for prolonged, uninterrupted periods.

Lake Economy

The lake economy consisted of Yellowstone Lake tributaries that supported spawning cutthroat trout (*Salmo clarki*) used as food by grizzlies. The economy functioned in the south, southeast, and Flat Mountain arms of the lake.

The food items contributing to the diet in the lake economy were similar in 1973 and 1974 but differed in rank and importance value, probably because of sampling differences. During the 2-year period, grass and cutthroat trout were the most important foods.

The feeding cycle was directly related to spawning activities of cutthroat trout, which extended from late June to early August. Time of occurrence of spawning trout varied among individual tributaries (Knight 1975).

Feeding activity was observed along a tributary at the tip of Flat Mountain Arm during the last half of July 1974. Estimated flow in the steam was 0.13 m^3/second, and estimated peak fish density was 6 fish per linear meter within 0.8 km of the mouth. Cutthroat trout in this segment averaged 38 cm in length and 0.6 kg in weight. Eleven different grizzlies were sighted fishing in the vicinity between 16 July and 18 July 1974 (Knight 1975). Grass, horsetail (*Equisetum arvense*), and elk thistle were heavily grazed in the area. Grizzly

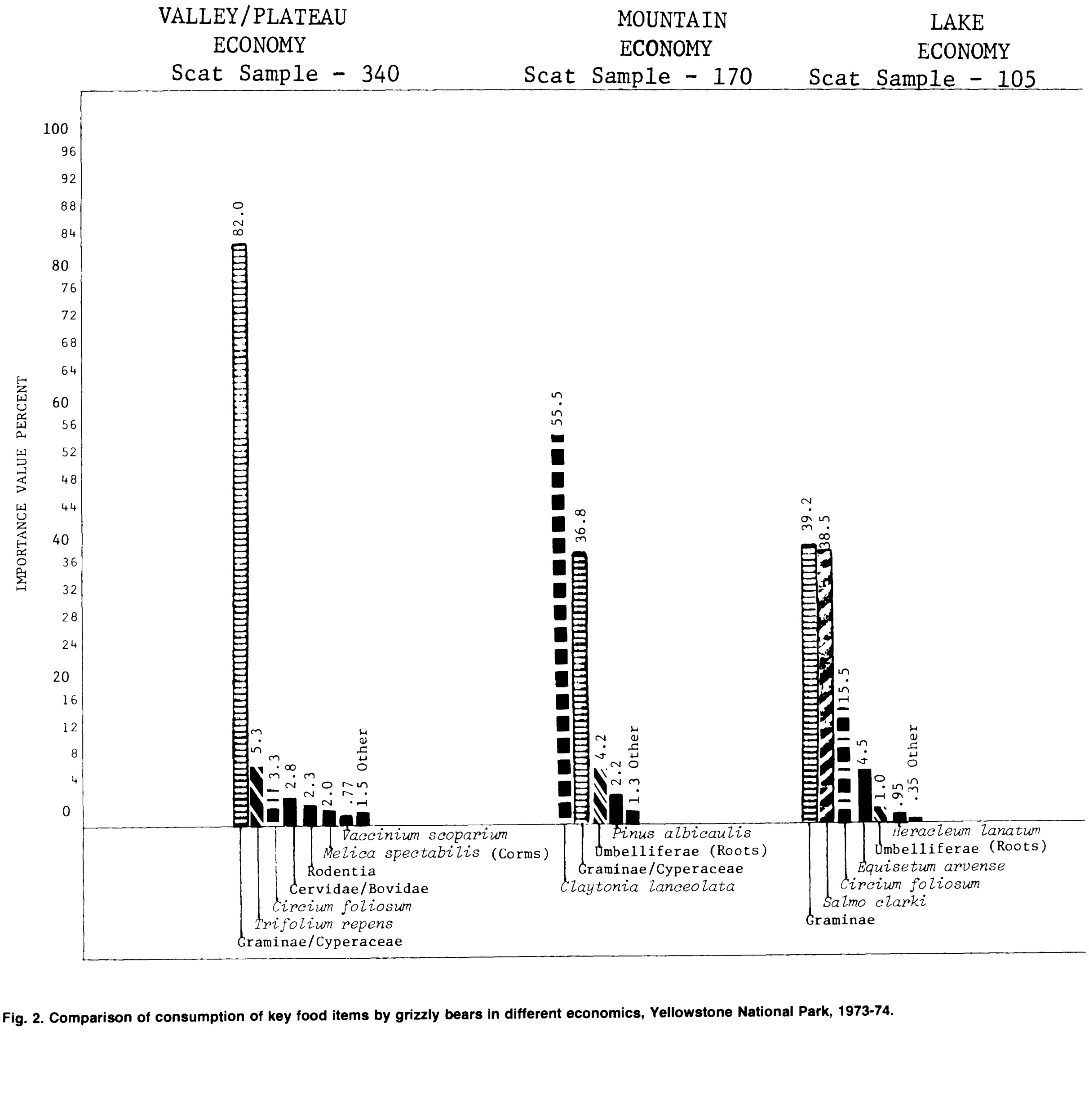

Fig. 2. Comparison of consumption of key food items by grizzly bears in different economics, Yellowstone National Park, 1973-74.

feeding activity was related to fish density in the tributary. On 2 August, peak fish density was estimated to be 0.5 fish per linear meter, and no fresh evidence of grizzly feeding was apparent.

Summaries

The 2-year summaries of food consumption for each of the economies show that grasses and sedges were the most important items in the valley/plateau economy, western springbeauty was the most important item in the mountain economy, and grass and cutthroat trout were the most important items in the lake economy (Fig. 2). The 3 economies were apparently oriented to: grasses and rodents (valley/plateau); springbeauty, grasses, and roots (mountain); and grasses and trout (lake).

Parkwide, the diet for each year was fairly constant. For the 2-year period, grasses and sedges were the top-ranked foods, with an importance value percentage of 78.5 (Table 1). Five of the 8 ranking food items were plants that represented 93.1 percent of total importance. The remaining 3 items, fish and mammals, represented 4.3 percent of the total importance value. Western springbeauty appeared to be the most highy selected of the major foods.

Food Quality and Apparent Digestibility

Five different samples of grass and grasses/sedges

Table 1. Summary of grizzly bear food consumption parkwide, Yellowstone National Park, 1973-74.

Food item	Use	Elevation (m)	Frequency occurrence percent	Percent composition per item	Percent of diet volume	Importance value	Importance value percent
Gramineae/Cyperaceae	Gramineae 95% stems leaves *Carex* sp. 5% heads	2,428	64.5	55.3	*35.70*	23.00000	*78.5000*
Claytonia lanceolata	Entire	2,821	15.1	79.9	*12.10*	1.80000	*6.1000*
Cirsium foliosum	Stems/heads	2,388	16.3	49.4	*8.00*	1.30000	*4.4000*
Trifolium repens	Stems/leaves/heads	2,369	11.0	57.0	*6.30*	0.69000	*2.4000*
Salmo clarki	Entire	2,376	9.3	57.8	*5.40*	0.50000	*1.7000*
Umbelliferae	*Perideridia gairdneri* 54% — roots *Lomatium cous* 46% — roots	2,525	10.9	41.6	*4.50*	0.49000	*1.7000*
Rodentia	*Thomomys talpoides* 63% *Microtus* spp. 35% *Marmota flaviventris* 2%	2,354	9.8	38.7	*3.80*	0.37000	*1.3000*
Cervidae/Bovidae	*Cervus canadensis* 90% *Odocoileus hemionus* 6% *Bison bison* 4%	2,318	8.1	56.5	*4.60*	0.37000	*1.3000*
Melica spectabilis	Corms	2,341	6.0	59.6	*3.60*	0.22000	*0.7500*
Equisetum arvense	Stems	2,409	5.5	49.3	*2.70*	0.15000	*0.5100*
Pinus albicaulis	Nuts	2,568	5.0	55.2	*2.80*	0.14000	*0.4800*
Vaccinium scoparium	Berries/leaves	2,408	4.2	63.4	*2.70*	0.11000	*0.3700*
Formicidae	Mature/larvae	2,504	8.8	9.6	*0.84*	0.07000	*0.2400*
Heracleum lanatum	Stems/leaves	2,463	3.1	47.1	*1.50*	0.04000	*0.1400*
Polygonum bistortoides	Entire	2,380	3.3	19.5	*0.63*	0.02000	*0.0700*
Russula sp.	Caps/stems	2,430	2.3	25.7	*0.59*	0.01000	*0.0300*
Fragaria virginiana	Fruits	2,447	1.6	18.4	*0.30*	0.00500	*0.0200*
Garbage		2,373	0.81	70.0	*0.57*	0.00500	*0.0200*
Taraxacum sp.	Stems/leaves/heads	2,426	0.81	54.0	*0.44*	0.00400	*0.0100*
Smilacina sp.	Rhizomes	4,447	0.65	71.3	*0.47*	0.00300	*0.0100*
Agoseris sp.	Stems/leaves/heads	2,223	0.49	76.6	*0.37*	0.00200	*0.0070*
Vespidae	Mature/larvae	2,347	0.65	24.1	*0.16*	0.00100	*0.0030*
Ribes setosum	Berries	2,621	0.33	100.0	*0.33*	0.00100	*0.0030*
Chlorophyceae	Entire	2,256	0.33	75.0	*0.24*	0.00080	*0.0030*
Forb — unidentified	Stems/leaves	2,149	0.33	75.0	*0.24*	0.00080	*0.0030*
Ranunculus sp.	Stems/leaves/flowers	2,405	0.49	30.0	*0.15*	0.00070	*0.0020*
Mertensia ciliata	Stems/leaves	2,842	0.33	50.0	*0.16*	0.00050	*0.0020*
Angelica sp.	Stems/leaves	2,408	0.33	27.5	*0.09*	0.00030	*0.0010*
Aster integrifolius	Stems/leaves	2,377	0.16	95.0	*0.15*	0.00020	*0.0007*
Pastinaca sativa	Stems/leaves	2,713	0.16	50.0	*0.08*	0.00010	*0.0003*
Ruppia pectinata	Stems/leaves	2,347	0.33	12.5	*0.04*	0.00010	*0.0003*
Anacharis sp.	Entire	2,377	0.16	20.0	*0.03*	0.00005	*0.0002*
					99.58	29.30455	*100.0755*

were analyzed along with corresponding scat material (Table 2). Protein was the primary nutrient utilized and the greatest source of energy. Protein digestibility of these samples compared favorably with the 54±12 percent reported for ruminants on roughage feeds including various grasses, legumes, and native western hay (Crampton and Harris 1969).

All 5 grasses and grasses/sedges were succulent when collected. The first 2 were collected before flowering, the last 3 after flowering. Protein content of preflowering material was higher than that of postflowering material; the opposite was true of nitrogen-free extract. Energy per gram generally remained constant. The data suggest a direct relationship between protein content and apparent protein digestibility. Highest protein digestibility was recorded for the higher protein content of preflowering samples; lowest protein digestibility was recorded for the lower protein content of postflowering samples. This result was to be expected because protein levels are highest in the aerial parts of plants during early growth stages, and plant cell contents at that time are most available for digestion before cell walls lignify (Klein 1965, Crampton and Harris 1969).

If values for nitrogen-free extract are accepted, a direct relationship between extract content and digestibility is also suggested. Apparent digestibility per gram of gross energy was fairly constant in spite of the differences in the relative amounts of protein and nitrogen-free extract and in their respective digestibilities. This finding suggests a digestive flexibility in grizzlies that may have provided a relatively constant energy intake regardless of changes in diet levels of protein and nitrogen-free extract.

Food quality of western springbeauty averaged 29.9 percent protein, 3.9 percent ether extract, and 45.7 percent nitrogen-free extract, which averaged 3.8 percent starch and 41.9 percent nonstarch. Calculated energy averaged 4.0 kcal/g. Digestibility of individual items averaged 61.8 percent for protein, 93.0 percent for starch, unknown for nonstarch nitrogen-free extract (7.5 percent if the values are accepted), and 30.5 percent per gram of gross energy (35.0 percent if nonstarch nitrogen-free extract values are accepted). Protein was the greatest energy source.

Averaged values for protein and ether extract content and digestibility for cutthroat trout were substantially higher than those recorded for succulent herbs. Ether extract of fish consisted primarily of triacylglycerols, which are the major components of storage fats in plant and animal cells; ether extract of the aerial portions of succulent herbs was probably made up primarily of phospholipids from cell membranes serving as structural elements (Lehninger 1973). Storage fats were more digestible than the waxy structural elements.

Averaged values for food quality and digestibility of Umbelliferae roots, melica and western springbeauty corms indicated that starch was a highly digestible energy-rich nutrient.

A summary of quality and digestibility of the most important grizzly foods indicates that animal material had the highest digestibility and the highest calculated energy content, and plant material had the lowest (Table 3). A direct relationship between food energy and digestibility is apparent; the higher the energy of the food, the greater its digestibility. Differential digestibility of plant and animal foods is apparent.

Nutritive Values

Five principal nutrient materials contributed to total energy intake of grizzlies. Protein from succulent herbs was estimated to be 42.8 percent digestible, protein and fat from animal material 78.1 percent digestible, fat and protein from whitebark pine nuts 73.6 percent digestible, and starch from herbs 78.8 percent digestible. The digestibility of sugar from berries and fruits of shrubs and herbs was undetermined but assumed to be high.

Seasonal grizzly nutritive values for 1974 were compared among the 3 economies. Each economy had a unique nutritional plane. The valley/plateau economy was nutritionally distinguished by the relatively high nutritive value of protein from succulent herbs. The mountain economy was distinguished by the relatively high nutritive value of starch, and the lake economy by the relatively high nutritive value of protein and fat from fish. Protein from succulent herbs appeared to be the primary and sustaining nutrient in all 3 economies.

For the 2-year period in the Park, protein from succulent herbs, with a nutritive value of 77.3 percent, was the grizzlies' most important source of energy (Fig. 3). Protein and fat from animal material ranked second, starch ranked third, and fat and protein from whitebark pine nuts ranked fouth. Energy contribution of sugar from fruits and berries is unknown, but its nutritive value percentage probably did not exceed 0.50.

DISCUSSION

In Yellowstone Park, grizzlies occupied fertile, primarily open grasslands, herblands, and parklands with adequate cover where protein, taken in large quantities primarily from succulent herbs and secon-

Table 2. Quality and digestibility of grizzly bear foods as indicated by chemical analysis.

Item: Gramineae/Cyperaceae
Consumption rank: 1
Importance value percent: 78.5

	Whole food material		Corresponding scat material		
	Proximate content	Calculated gross kcals	Apparent digested kcals	Concentration factor	Apparent digestibility percent
Item: *Agropyron* sp. — 50%, *Poa* sp. — 20%, *Bromus* sp. — 10%, *Phleum alpinum* — 10%, *Carex* sp. — 10% Economy: Mountain Condition: Preflowering, succulent					
Protein	22.9	128.2	63.8	0	49.8
Ether extract	3.7	34.4	Unknown	1.2	Unknown
Nitrogen-free extract	39.4	169.4	Unknown	Unknown(1.01)[a]	Unknown
Total		332.0	63.8		
Per gram		3.3	0.64		19.4
Item: *Poa* sp. — 50%, *Agropyron* sp. — 30%, *Phleum alpinum* — 10%, *Carex* sp. — 10% Economy: Mountain Condition: Preflowering, succulent					
Protein	25.6	143.4	68.9	0	48.0
Ether extract	3.6	33.5	Unknown	1.3	Unknown
Nitrogen-free extract	35.9	154.4	Unknown	Unknown (1.1)	Unknown
Total		331.3	68.9		
Per gram		3.3	0.69		20.9
Item: *Deschampsia caespitosa* — 80%, *Carex* sp. — 20% Economy: Mountain Condition: Postflowering, succulent					
Protein	14.0	78.4	31.9	0	40.7
Ether extract	2.7	25.1	Unknown	1.1	Unknown
Nitrogen-free extract	46.8	201.2	Unknown (24.5)	0	Unknown (12.2)
Total		304.7	31.9 (56.4)		
Per gram		3.0	0.32 (0.56)		10.7 (18.8)
Item: *Poa* sp. — 100% Economy: Valley/plateau Condition: Postflowering, succulent					
Protein	17.4	97.4	35.8	0	36.7
Ether extract	1.5	13.9	Unknown	1.9	Unknown
Nitrogen-free extract	62.2	267.5	Unknown (73.9)	0	Unknown (27.6)
Total		378.8	35.8 (109.7)		
Per gram		3.7	0.36 (1.1)		9.5 (28.9)
Item: *Calamagrostis canadensis* — 100% Economy: Valley/plateau Condition: Postflowering, succulent					
Protein	17.6	98.6	34.2	0	34.7
Ether extract	5.0	46.5	27.0	0	58.0
Nitrogen-free extract	41.9	180.2	Unknown (3.9)	0	Unknown (2.2)
Total		325.3	61.2 (65.1)		
Per gram		3.3	0.61 (0.65)		18.5 (19.7)

Averaged values					
Protein	19.5	109.2	46.9	0	42.0
Ether extract	3.3	30.7	5.4	1.1	11.6
Nitrogen-free extract	45.2	194.5	Unknown (20.5)	0	Unknown (8.4)
Total		334.4	52.3 (72.8)		
Per gram		3.3	0.52 (0.73)		15.8 (21.5)

[a] Nitrogen-free extract values are determined by difference and are subject to possible error. Results in this category are recorded as Unknown. Numerical values are given in this category and elsewhere in parentheses to show the result if the values are accepted.

Table 3. Summary of the quality and digestibility of grizzly bear food items.

Food item	Apparent digested kcals/g	Apparent digestibility percent	Calculated kcals/g whole food	Consumptive use rank
Cervidae/Bovidae	4.6	81.3	5.6	8
Salmo clarki	4.1 (4.2) [a]	73.2 (73.7)	5.7	5
Pinus albicaulis (nuts)	1.9 (2.1)	48.7 (52.5)	3.9	11
Claytonia lanceolata	1.2 (1.4)	30.5 (35.0)	4.0	2
Umbelliferae (roots) plus corms of *Melica spectabilis* and *Claytonia lanceolata*	1.0 (1.5)	25.7 (36.8)	3.9	6
Russula sp.	0.98 (1.3)	25.0 (33.0)	3.9	16
Gramineae/Cyperaceae	0.52 (0.73)	15.8 (21.5)	3.3	1
Trifolium repens	0.50 (0.79)	13.9 (21.9)	3.6	4
Equisetum arvense	0.37	12.8	2.9	10

[a] Results in parentheses include nitrogen-free extract values.

darily from artiodactyls, satisfied most of their energy needs. These needs were met because protein is convertible to fat and ketone bodies via the intermediary metabolism; such conversion occurs particularly when protein is taken in excess (Lehninger 1973). Because of their nutritional dependence on protein, Yellowstone grizzlies in 1973-74 occupied primarily a protein food niche.

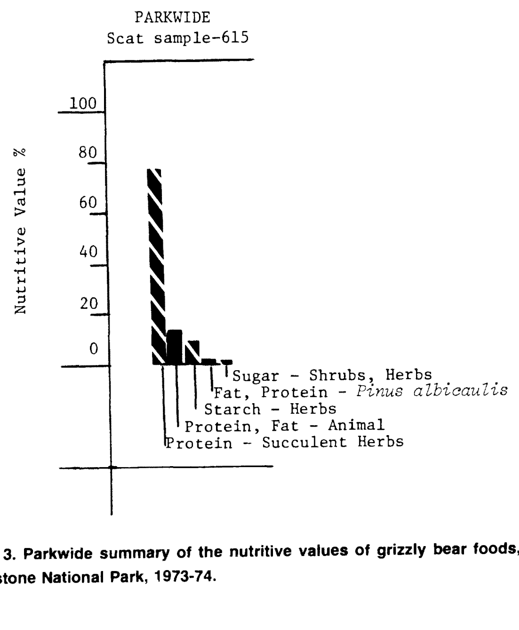

Fig. 3. Parkwide summary of the nutritive values of grizzly bear foods, Yellowstone National Park, 1973-74.

In this study, park grizzlies grazed for long periods on grasslands. Protein digestibility of grassland herbs was 42.8 percent, considerably lower than the indicated digestibilities of the other principal nutrient materials. Park grizzlies compensated for this relatively low nutrient digestibility by a high intake of succulent herbs that insured a high level of ingested protein and a consequent energy source and fat store. Geist (1974:207) noted a similar process in the perissodactyl, which can "compensate for poor forage of low digestibility by eating more and passing out the undigested portions relatively quickly. It can thus maintain a steady stream of energy and nutrients across the gutwall, but does so by digesting the forage less efficiently than do ruminants and by consuming more forage."

Davis (1964) discussed gut length and dentition of the Ursidae, and Hoffman and Pattie (1968) and Greer and Craig (1971) described both the teeth and feet of grizzly bears. Colbert (1969) discussed the adaptive significance of ursid dentition. Carnassial shearing teeth are absent in grizzlies (and all other bears) and have been replaced by crushing bunodont molars, an apparent adaptation to an herbivorous or omnivorous diet. The front claws of grizzlies are longer than 55 mm, allowing these bears to be effective diggers, possibly an additional adaptation to herbivory. The food niche (primarily plant protein) occupied by Yellowstone grizzlies is attributable in part to their relatively long gut length, bunodont molars, and long claws. These physical characteristics allowed utilization of plant materials without preventing a high digestibility of animal material. As a result, grizzlies were digestively flexible and were able to make maximum use of both plant and animal protein. This digestive flexibility accounted in part for the successful exploitation of the park's 3 different food economies.

Yellowstone grizzlies appeared to be adapted primarily to the most constant and abundant protein sources in their environment. Fertile grasslands and herblands provided a constant supply of protein because a relatively large portion of fixed light energy was available as food energy directly in succulent herbs and indirectly in herbivores. Conferous forests did not provide such rich souces of energy. In 1974, seasonal foods such as pine nuts and berries were relatively abundant and contributed importantly to the grizzly diet. In 1973, pine nuts and berries were not abundant and were relatively scarce in the diet. A periodic low annual production of nuts and berries, such as occurred in 1973, probably has no major impact on park grizzlies because nutritionally they are anchored to the more stable energy supply available from grasslands, herblands, and associated forested edges.

Relative scarcity of animal foods during the pregreen-up period probably sets absolute limits on the protein available to grizzlies at this time. This limited protein availability could in turn limit grizzly numbers when their demand for animal protein exceeds the supply. At such times, competition among grizzlies for animal food (Cole 1972) may result in population losses. Dispersal and direct mortality may cause losses among subordinate bears (Stokes 1970, Martinka 1976). The pregrowing season is the only time in the park when bears' supply of protein could be strictly limited. This period is likely to be the primary one in which natural regulation of grizzly populations occurs.

The grizzly population in the park has been estimated to be 178-270; the highest density, excluding the Yellowstone Lake area, has been estimated to be 1 bear per 5.7 km^2 in Hayden and Pelican valleys (Knight 1974). These estimates indicate a lower population level and a lower density than might otherwise be expected of an animal population at the primary consumer level in pristine grassland habitat (Odum 1971). Two explanations at least partially account for the grizzly population level and densities in the park:

1. Grizzlies are secondary consumers during pregreen-up periods, when they are probably subject to population-limiting pressures related to the amounts of available animal protein.
2. Grizzlies are relatively inefficient grazers because of their dentition and digestive structure. Hence, the available supply of areas providing the tall, dense stands of succulent protein-rich herbs that grizzlies require probably has a limiting effect on grizzly numbers.

Grizzly digestive capability with respect to succulent herbs was limited primarily to the extraction of protein. By comparison, artiodactyls digest protein, ether extract, fiber, and nitrogen-free extract from herbs in nearly any condition (Crampton and Harris 1969) and consequently obtain more energy per gram of vegetation than do grizzlies. To maximize energy intake and compensate for low energy per gram of forage, grizzlies sought out and ingested large quantities of succulent herbs growing in tall, dense stands. Such high-quality stands were extensive in the park but not unlimited.

Nutritionally, free-ranging Yellowstone grizzlies using natural foods were primarily herbivores and secondarily carnivores in 1973-74, obtaining protein from succulent herbs and artiodactyls. Digestive flexibility permitted maximum protein use of both plant and animal foods. The principal environmental requirement necessary for continued support of grizzlies in their multi- and mixed-level trophic niche appeared to be the availability of grasslands and herblands capable of maintaining elk and bison in sufficient numbers to provide adequate food for pregreen-up secondary consumption, of providing rodents for growing-season mixed consumption, and plentiful, succulent and nutritious herbs for growing- and postgrowing-season primary and mixed consumption.

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