



The natural food habits of free ranging grizzly bears in Yellowstone National Park, 1973-1974
by Stephen Patrick Mealey

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE
in Fish and Wildlife Management
Montana State University
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Abstract:

The natural food habits of free-ranging grizzly bears in Yellowstone National Park were investigated in 1973-1974 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. The results supported the hypothesized existence of three distinctive mixes of physiographic and biotic conditions or feeding economies: the valley/plateau economy, a grass/rodent economy where grizzlies were intensive diggers; the mountain economy, primarily a grass/springbeauty/root economy where grizzlies were casual diggers; and the lake economy, primarily a fish/grass economy where grizzlies were fishers. The feeding cycle in the valley/plateau and mountain economies appeared to follow plant phenology. Grizzlies fed primarily on meat before green-up and on succulent herbs after; meat, corns, berries and nuts became important during the post-growing season. Distribution was directly related to fertile soils and the occurrence of succulent herbs. Succulent grasses and sedges with an importance value percent of 78.5 were the most important food items consumed. Protein from animal tissue was more digestible than protein from plant tissue. In plants, storage fats were more digestible than structural fats. Food energy and digestibility were directly related. Five principal nutrient materials (listed with their percent digestibility) 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 percent of 77.3 was the grizzly's most important energy source. Succulent, pre-flowering 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 compensated for by high intake. Grizzlies were digestively flexible and maximized use of protein from plant and animal sources. They appeared to be adapted to the most constant and abundant protein sources: succulent herbs and animal material from open, fertile grasslands. Competition among grizzlies for animal material during the pre-growing season may have regulatory consequences for the grizzly population. The Park's grizzly population level can be partially accounted for by the apparent facts that grizzlies are secondary consumers during pre-green-up periods and that they are relatively inefficient primary consumers during the growing and postgrowing seasons. Grizzlies occupied a trophic niche which included primary and secondary consumer levels and a mixture of both. The essential environmental requirement was the availability of fertile grasslands capable of maintaining artiodactyls, rodents and abundant nutritious herbs as potential food.

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Date

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by

STEPHEN PATRICK MEALEY

A thesis submitted in partial fulfillment
of the requirements for the degree

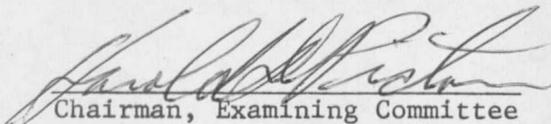
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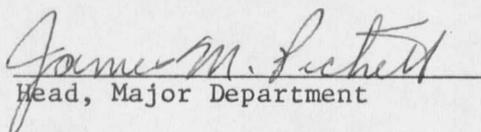
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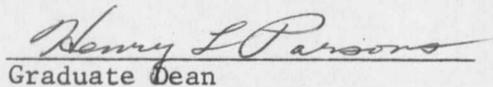
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Chairman, Examining Committee


Head, Major Department


Graduate Dean

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ABSTRACT

The natural food habits of free-ranging grizzly bears in Yellowstone National Park were investigated in 1973-1974 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. The results supported the hypothesized existence of three distinctive mixes of physiographic and biotic conditions or feeding economies: the valley/plateau economy, a grass/rodent economy where grizzlies were intensive diggers; the mountain economy, primarily a grass/springbeauty/root economy where grizzlies were casual diggers; and the lake economy, primarily a fish/grass economy where grizzlies were fishers. The feeding cycle in the valley/plateau and mountain economies appeared to follow plant phenology. Grizzlies fed primarily on meat before green-up and on succulent herbs after; meat, corms, berries and nuts became important during the post-growing season. Distribution was directly related to fertile soils and the occurrence of succulent herbs. Succulent grasses and sedges with an importance value percent of 78.5 were the most important food items consumed. Protein from animal tissue was more digestible than protein from plant tissue. In plants, storage fats were more digestible than structural fats. Food energy and digestibility were directly related. Five principal nutrient materials (listed with their percent digestibility) 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 percent of 77.3 was the grizzly's most important energy source. Succulent, pre-flowering 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 compensated for by high intake. Grizzlies were digestively flexible and maximized use of protein from plant and animal sources. They appeared to be adapted to the most constant and abundant protein sources: succulent herbs and animal material from open, fertile grasslands. Competition among grizzlies for animal material during the pre-growing season may have regulatory consequences for the grizzly population. The Park's grizzly population level can be partially accounted for by the apparent facts that grizzlies are secondary consumers during pre-green-up periods and that they are relatively inefficient primary consumers during the growing and post-growing seasons. Grizzlies occupied a trophic niche which included primary and secondary consumer levels and a mixture of both. The essential environmental requirement was the availability of fertile grasslands capable of maintaining artiodactyls, rodents and abundant nutritious herbs as potential food.

INTRODUCTION

A study of the natural food habits of free-ranging grizzly bears (*Ursus arctos horribilis*) Ord (Rausch, 1963) in Yellowstone National Park was conducted in 1973 and 1974 as part of the research effort of the Interagency Grizzly Bear Study Team in the Yellowstone ecosystem.

Extensive grizzly bear use of unnatural foods (garbage and camp groceries) in Yellowstone National Park occurred 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, 1971). After the removal of the primary sources of unnatural foods in the Park, most grizzlies resumed free-ranging use of natural foods (Cole, 1974).

Martinka (1974, 1970), Sumner and Craighead (1973), Cole (1972), Macpherson (1965), Murie (1961) and Murie (1944) have discussed grizzly bear food use. Seton (1953) reviewed the food use of all four North American species of bears. This study presents a description and analysis of the natural food use of free-ranging grizzlies in Yellowstone Park which has been absent from the literature.

The overall objective of my research was to develop hypotheses about the grizzly's: 1) natural energy sources and trophic level(s); 2) quality and quantity of nutrient use; and 3) distribution.

Specific research objectives were to: 1) identify by season and location the type and relative quantitative importance of natural food

items; 2) estimate food quality, efficiency of food use, seasonal nutrient intake and nutritive values of the principal nutrient materials; 3) explore the relationship between distribution and the different physiographic/vegetative units of the Park; 4) describe the head and body lengths, and the stomachs and intestinal tracts of deceased grizzlies utilized as study specimens; 5) report general observations on feeding activities; and 6) develop a summary sketch of the generalized trophic niche of Yellowstone grizzly bears.

THE STUDY AREA

General

Yellowstone National Park occupies about 8900 km.² in the states of Wyoming, Montana and Idaho (Figure 1). The Park was established March 1, 1872 (17 Stat. 32), and "dedicated and set apart as a public park or pleasuring-ground for the benefit and enjoyment of the people" and "for the preservation, from injury or spoilation, of all timber, mineral deposits, natural curiosities, or wonders ... and their retention in their natural condition." In contemporary terms its purpose is: "to perpetuate the natural ecosystems within the Park in as near pristine conditions as possible for their inspirational, educational, cultural and scientific values for this and future generations" (National Park Service, 1973). Accordingly, management programs, including the removal of unnatural food sources from bears, have been undertaken to minimize the impact of man on all components of the Park.

In 1971, 99 percent of the Park's 899,139 ha. remained roadless and 88.4 percent of the area was found suitable for preservation as wilderness (National Park Service, 1971).

Physiography

The geology of the Park has been described by Keefer (1972) and Eaton *et al.* (1975), the climate by Lowery (1959), and the



Figure 1. Map of the study area, Yellowstone National Park.

vegetation zones by Despain (1973b).

The Paleozoic and Mesozoic sediments, the Absaroka andesitic volcanics, and the Yellowstone rhyolitic volcanics are the three major types of substrate left by the Park's past geologic events (Figure 2). Disintegration in place of these substrates resulted in three unique soil types in the Park. Transported soils from glacial, lacustrine and alluvial action represent a fourth type (Figure 2).

Soils derived from Paleozoic and Mesozoic sediments are fertile and support a diverse plant community (Despain, 1973a). The spruce-fir (*Picea engelmannii* - *Abies lasiocarpa*) zone, dominated by spruce-fir forests, is endemic to these soils (Despain, 1973b; Figure 3). Whitebark pine (*Pinus albicaulis*) is present in the zone and is, in some cases, the dominant species, especially near timberline. Numerous species of grasses, sedges and forbs are present in the zone. They predominate in herblands and subalpine meadows and on mountain slopes and ridgetops. This zone lies above 2,560 m. and generally has greater than 102 cm. of precipitation annually, most falling as snow. The growing season extends from early June to late August and reflects the Park's short, cool summers and long, cold winters. The alpine-tundra zone also occurs on these soils above about 2,896 m. where low growing forbs are the predominant plant form.

Absaroka andesitic soils are fertile (Washington, 1917) and productive. The spruce-fir and alpine-tundra zones cover these soils

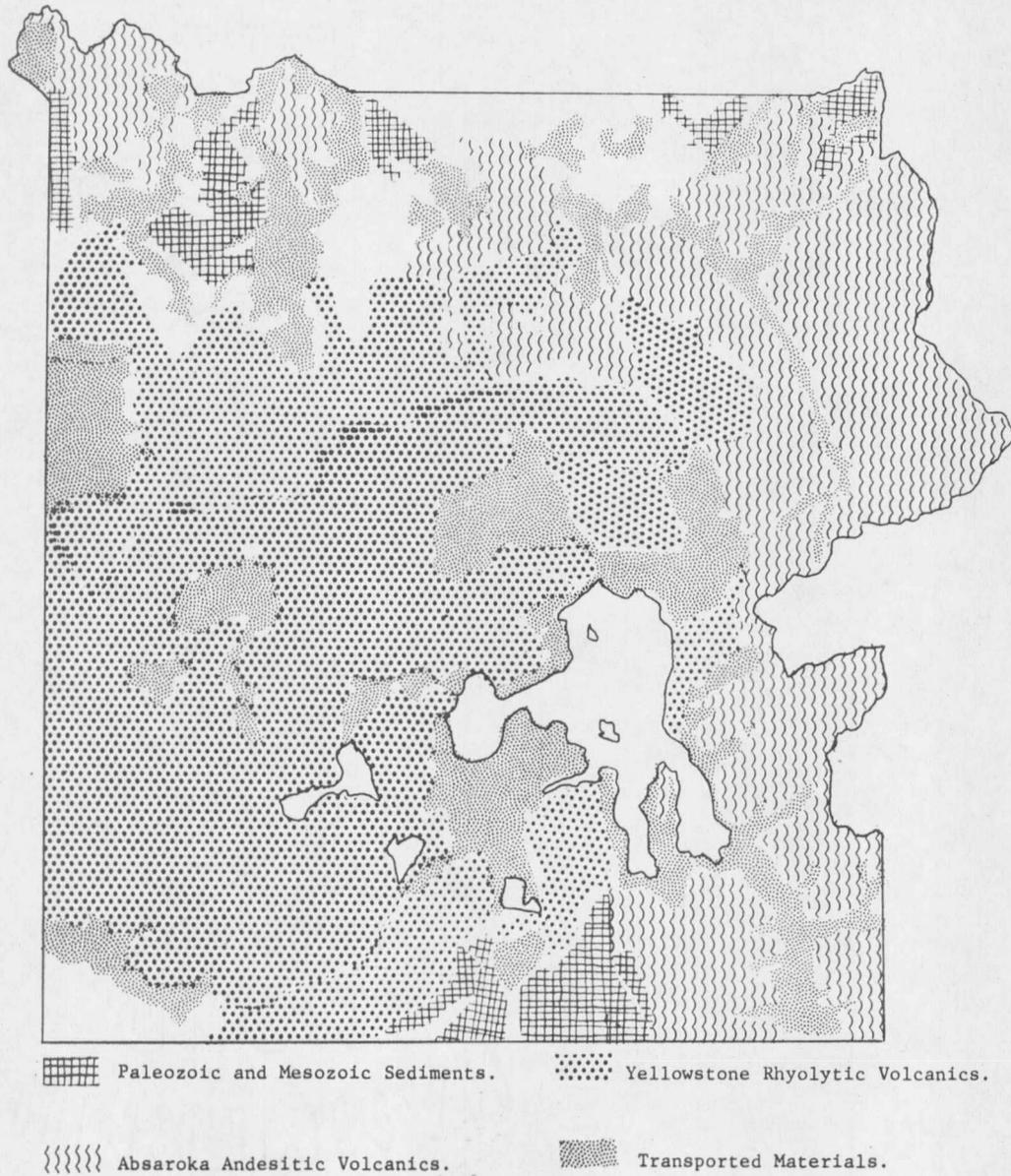
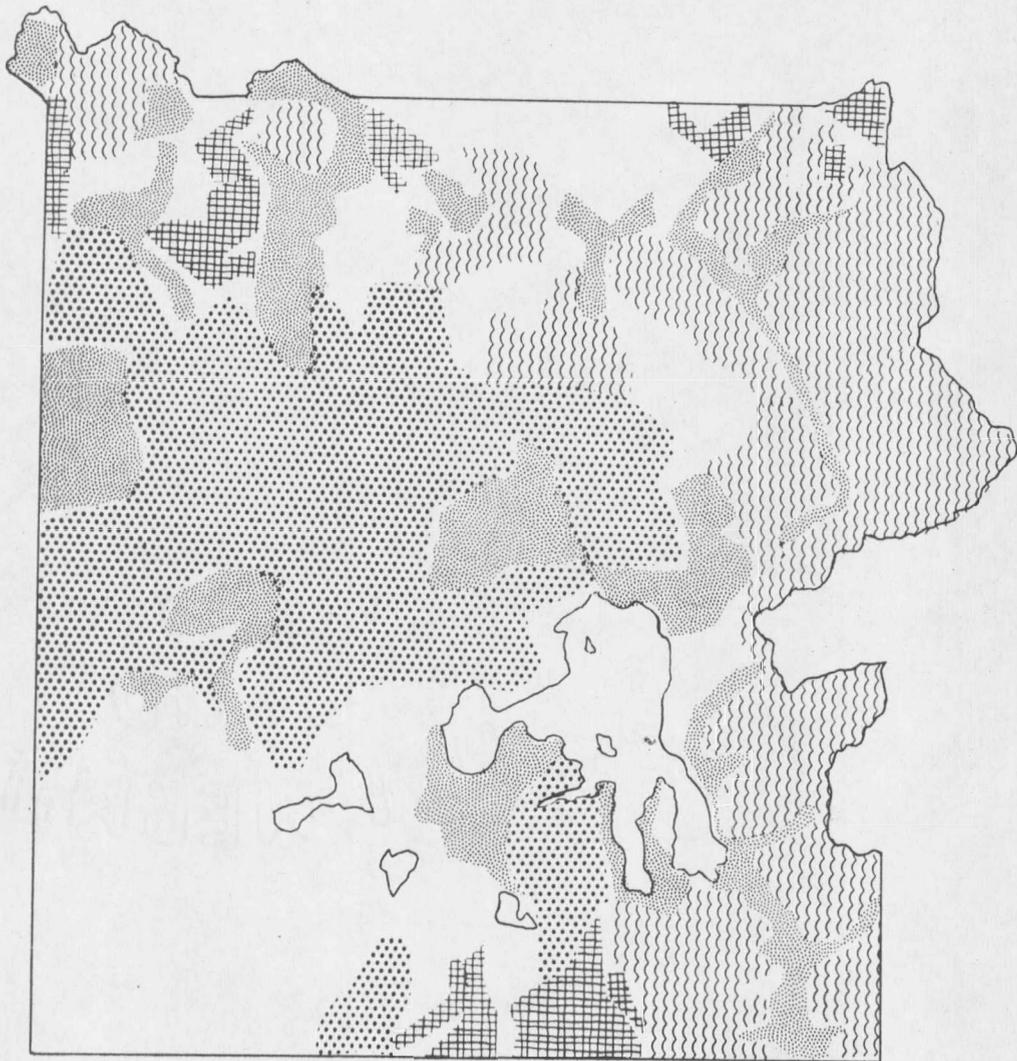


Figure 2. Map showing substrates from major geologic formations and activities in Yellowstone National Park (after Keefer).



	Fertile Paleozoic and Mesozoic Sedimentary Soils: Spruce-Fir Zone.		Infertile Rhyolytic Soils: Lodgepole Pine Zone.
	Fertile Andesitic Soils: Spruce-Fir Zone.		Fertile Transported Soils: Douglas-fir and Grassland Zones.

Figure 3. Map showing selected generalized soil and vegetation relationships in Yellowstone National Park (after Keefer and Despain).

(Despain, 1973b; Figure 3).

Yellowstone rhyolitic soils are infertile and do not support the growth of many plant types (Washington, 1917; Stermitz *et al.*, 1974). The lodgepole pine (*Pinus contorta*) zone is indigenous to rhyolitic soils and this species predominates as both a climax and a seral species (Despain, 1973b; Figure 3). Whitebark pine occurs in the zone and spruce and fir stands and small grasslands occur where moisture and soil conditions are favorable. This zone lies between 2,316 and 2,560 m. and receives 50-100 cm. of precipitation per year.

Transported soils deposited by ice and water were derived by the erosion of all three major substrate types. Generally, transported soils are fertile (Odum, 1971). These soils in the Park have relatively thick A horizons and are generally highly productive. The Douglas-fir (*Pseudotsuga menziesii*) zone occurs on these soils along the Yellowstone and Lamar River valleys (Despain, 1973b; Figure 3). Douglas-fir is the dominant forest type and big sagebrush (*Artemisia tridentata*) and various grasses, sedges and forbs cover the open areas. Aspen (*Populus tremuloides*), spruce, fir and lodgepole pine are also present. Grasses, sedges, forbs and big sagebrush grow on the transported soils of Hayden and Pelican Valleys, Cougar Creek Flat and Swan Lake Flat and other treeless areas. Precipitation and temperature vary over the areas with transported soils. Elevations range from 1,829 m. to 2,560 m., probably accounting for the differences in vegetation among

areas. The growing season on these soils extends generally from late May to early September.

The interactions among the Park's geologic events, climate, soils and vegetation have resulted in the three physiographic/vegetative units depicted in Figure 4. These are: 1) the mountainous unit with the spruce-fir and alpine-tundra zones covering fertile soils; 2) the valley and plateau units with fertile soils covered by grasslands and the Douglas-fir zone; and 3) the plateau unit with lodgepole pine covering infertile soils.

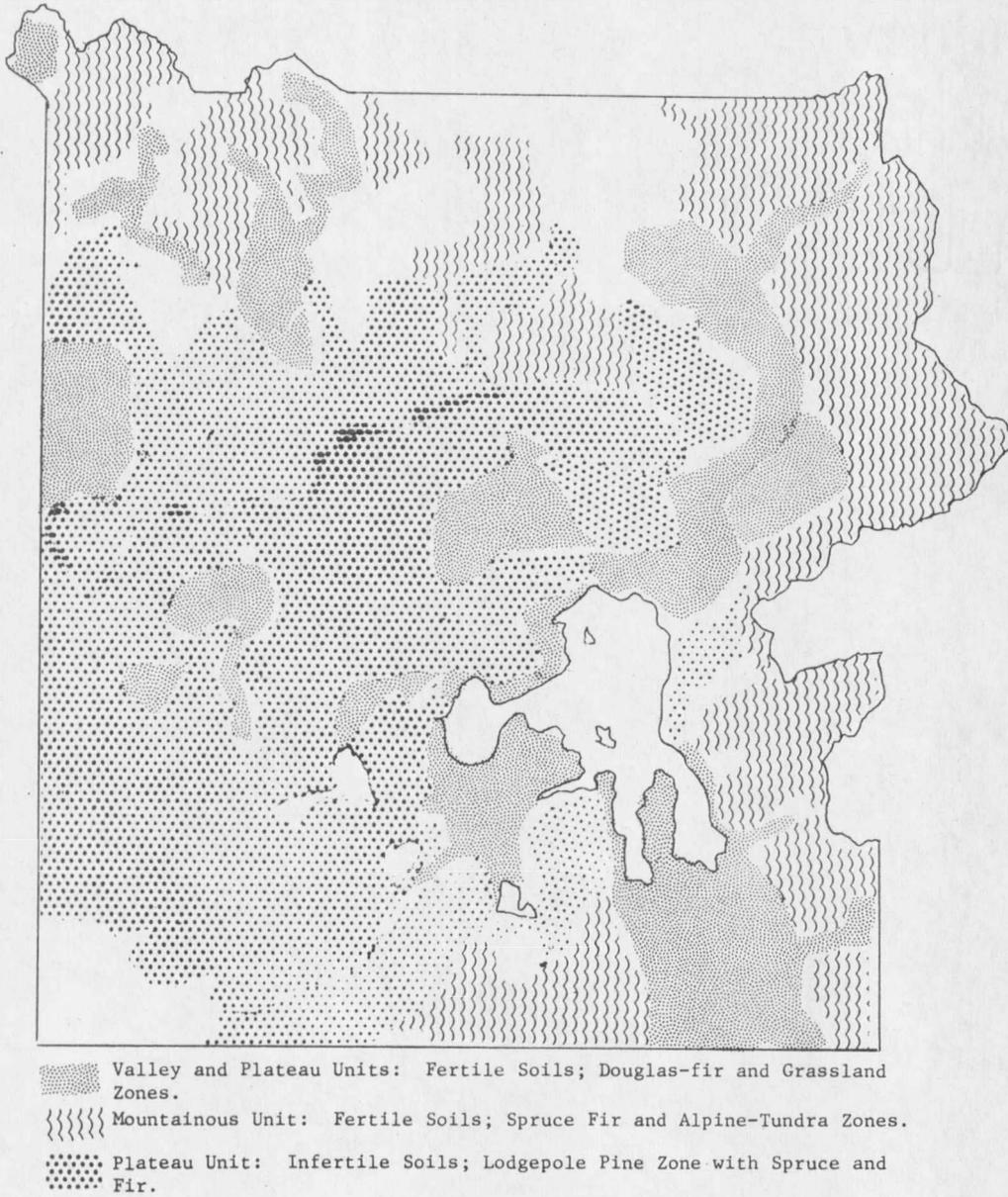


Figure 4. Map showing three generalized physiographic/vegetative units in Yellowstone National Park.

METHODS

Economy Concept

In the context of human culture an economy is understood to be an institutionalized process of exchange between producers and consumers (Peterson, 1971). The concept of economy as a process of exchange between producers and consumers can be applied to biologic systems including grizzly bears (consumers) interacting with their food sources (producers). In 1973 I hypothesized three unique feeding economies for grizzlies in the Park: the valley/plateau, mountain and lake economies. The basis for distinguishing these economies was the simultaneous occurrence of scats in each. After further study in 1974, each economy, in addition, seemed to represent a distinctive mix of physiographic and biotic conditions which appeared to result in a characteristic pattern of interactions between grizzlies and food items which was unique to each economy. Grizzlies in each economy seemed to have characteristic feeding activities which allowed them to maximize food use. Figure 5 shows the hypothesized economies. Designated areas represent centers of concentrated grizzly feeding activity determined by locations of scats collected in 1973 and 1974 (the Absaroka Range was not sampled). Areas of high grizzly density determined by aerial surveys are coincident (Knight, 1974, 1975). Grizzlies in the Park appeared to be distributed by economy.

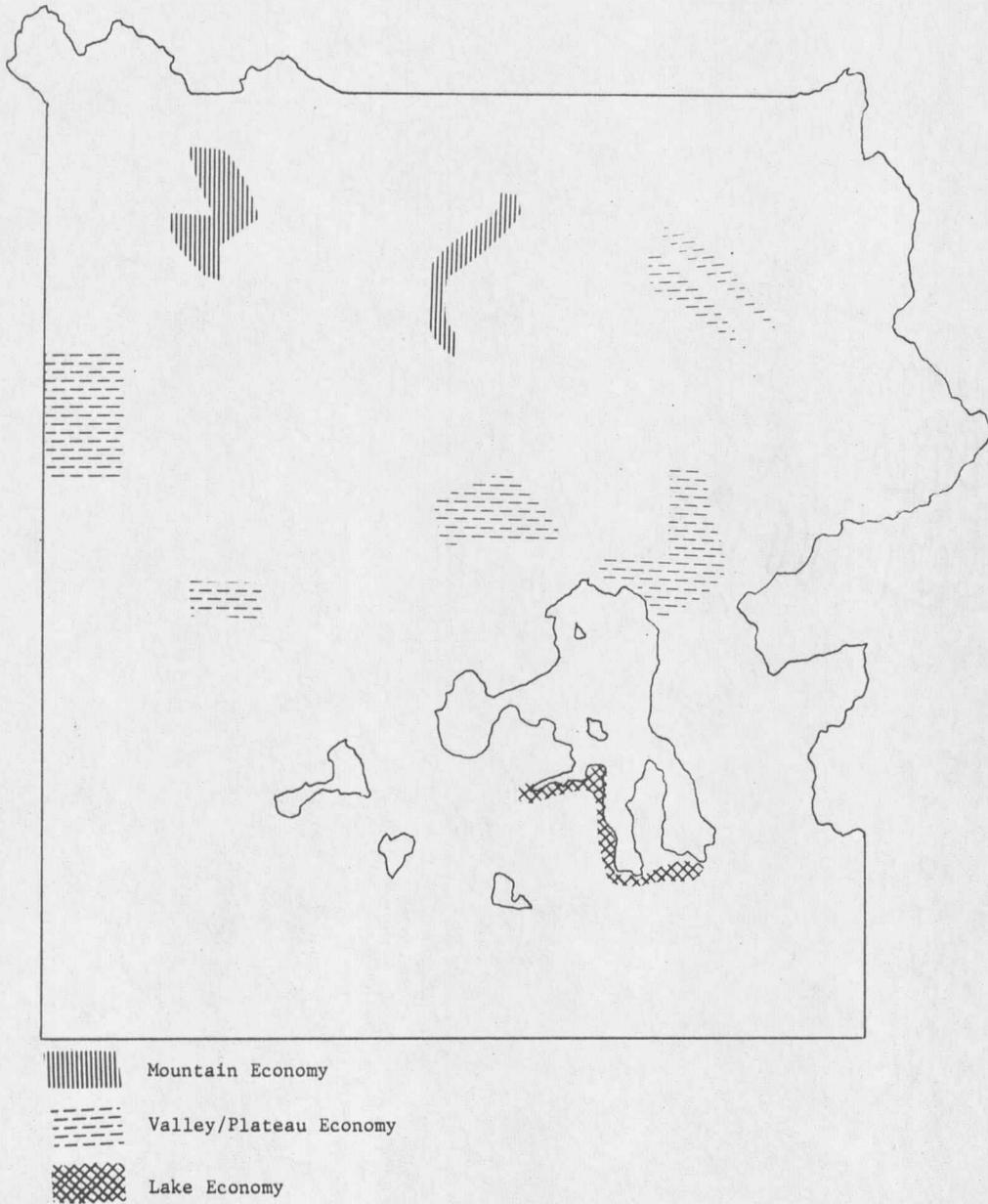


Figure 5. Map showing centers of generalized grizzly bear distribution in three different economies in Yellowstone National Park.

Quantitative Analysis: Scat Collection,
Preparation, and Analysis

Table 1 presents a summary of the scat collection effort. Travel in the roadless area of the Park was by horseback. Travel on Yellowstone Lake was by canoe.

Grizzly bear scats and visual observations of feeding activity were used in determining the quantitative importance of food items used by grizzly bears. Grizzly scats were usually distinguished from black bear scats on the basis of size; those with diameters 5 cm. or greater were normally considered to be grizzly (Murie, 1954). Several associations in the field between different grizzlies and their scats justified this approach. Other evidence considered in identifying scats was associated track sign, associated feeding activity sign, visual observations 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 they were found in an area generally associated with grizzly activity and some evidence of grizzly use was present.

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

approximate age. Age was estimated to the nearest month. Factors considered in age estimation were: state of scat desiccation and/or decay, presence and stage of maturity of insect eggs and/or larvae in the scat, growth status of vegetation under and around the scat and other associated and dateable evidence of grizzly activity. All scats were air dried for storage. Those scats which were extremely moist and/or infested with insect eggs and/or larvae were oven-dried at low heat to kill any organisms which could change the nature of scat contents.

Analysis of scat contents was conducted both in the field and in the laboratory. Field analysis was advantageous because scat contents were more identifiable when fresh and plant remains in the scats were usually represented by specimens growing nearby. 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 restore original form; 2) separation of material into homogeneous groups by use of screens (No. 10 and 20 mesh); 3) identification of contents; and 4) recording.

Identification to species, through macroscopic and microscopic examination, was usually successful for all items except grass. Reference collections of plants and seeds at the Montana Fish and Game

Department Wildlife Laboratory and the Montana State University Herbarium provided invaluable assistance in the identification process. The basic botanical references were *Flora of Montana, Part I*, by Booth (1950), *Flora of Montana, Part II*, by Booth and Wright (1959), and *Grasses of Montana*, by Booth (1972). Mammal remains were identified with the assistance of personnel at the Wildlife Laboratory. Basic references were *A Guide to Montana Mammals*, by Hoffmann and Pattie (1968) and *A Study of Identifying Characteristics of Mammal Hair*, by Spence (1963).

The occurrence and percent composition of each identified food item was recorded as each scat was analyzed. Percent composition denotes the percent of the total scat volume consisting of a single food item. Visual estimates of volume were recorded under one of four categories: trace - 25%; 25-50%; 50-75%; and 75-100%. This method of determining food use by estimation of scat composition by volume undervalued the use of some foods, because differential digestibility among food items was established through proximate analysis techniques. Animal material was found to be more digestible than most plant material.

Data were grouped and analyzed by the economy, month and year in which scats were collected. Data were also grouped in three categories which related grizzly food use and plant phenology. The latter included: pre-growing season, April 1-June 1; growing season, June 1-

September 1; and post-growing season, September 1-November 15. These periods approximately reflect plant growth conditions in the Park (Despain, 1974).

In grouped data presentations, food items are presented in rank order according to importance value calculated as:

$$\text{Importance Value} = \frac{\text{Frequency of Occurrence \%} \times \text{\% of Diet Volume}}{.01}$$

where Frequency of Occurrence Percent 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 average percent composition of an item which appeared 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 which occurred infrequently but in high volume percentages and items which occurred frequently but in low volume percentages. Importance value is convenient in providing a single unit of expression for frequency of occurrence and percent composition. Sumner and Craighead (1973) used a similar approach.

Percent Composition Per Item and Importance Value Percent were calculated. Percent compositions per item indicate the degree of selection for particular foods; values were derived by dividing the

average percent composition of those scats containing a given item by the total number of scats containing that food item. Importance value percents were derived by adding the importance values in the group and dividing individual values in the group by the sum. Importance value percents were calculated to facilitate comparison of food item importance values between and among groups.

Qualitative Analysis: Food Quality, Digestibility
and Nutritive Value

To estimate food quality, efficiency of food use, seasonal nutrient intake and nutritive values of the principal nutrients, determinations were made of: 1) the identities, energy values and apparent digestibilities of the principal nutrient materials of the most important foods listed in Table 23; 2) seasonal nutrient intake and nutritive value; and 3) plant protein/succulence-flowering relationship.

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 these principal nutrients. Apparent digestibility is a measure of nutrient utilization and digestive efficiency. It 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 four 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 non-dietary origin (Crampton and Harris, 1969); and 4) sampling error.

Food items and scats containing residues of these same items were collected at the feeding site. Scat and food item samples were paired and submitted to the Chemistry Station Analytical Laboratory at Montana State University for analysis. Analytical methods for proximate analysis followed the *Association of Official Agricultural Chemists Handbook* (1975).

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

Seasonal nutrient intake was calculated from 1974 seasonal food use data. Nutrient importance values were determined in a way similar to that presented for the determination of food item importance values.

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

$$\text{NVI} = \text{Nutrient Intake (Importance Value \%)} \times \text{Digestibility \%}$$

Nutritive value indices were converted to percents to facilitate comparisons.

The relationship between plant protein content and succulence-flowering condition was investigated by sampling and comparing vegetation from five plots in the Park. A protein loss factor was calculated to show the change in percent protein relative to percent crude fiber as vegetation completed reproduction and underwent desiccation. Protein Loss Factor, (PLF) was calculated according to the formula:

$$\frac{\text{Early } \frac{\% \text{ Protein}}{\% \text{ Crude Fiber}}}{\text{Late } \frac{\% \text{ Protein}}{\% \text{ Crude Fiber}}} = \text{PLF}$$

Grizzly Bear Anatomy

The fresh carcasses of two grizzlies were obtained for study. Head and body lengths and descriptions of stomachs and intestinal tracts are presented. Linear measurements were made with Vernier calipers and a meter stick. Head and body measurements were taken from tip of nose to the last vertebrae. Intestinal measurements were taken, with the mesentary removed, from the pyloric valve to the anus.

RESULTS

Quantitative: Food Item Consumption, General Observations, and Summaries

Valley/Plateau Economy

Major epicenters of the valley/plateau economy were Hayden, (Figure 6) Pelican and Lamar Valleys, and Cougar Creek Flat. Fertile, transported soils support an abundant grassland biota which 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.

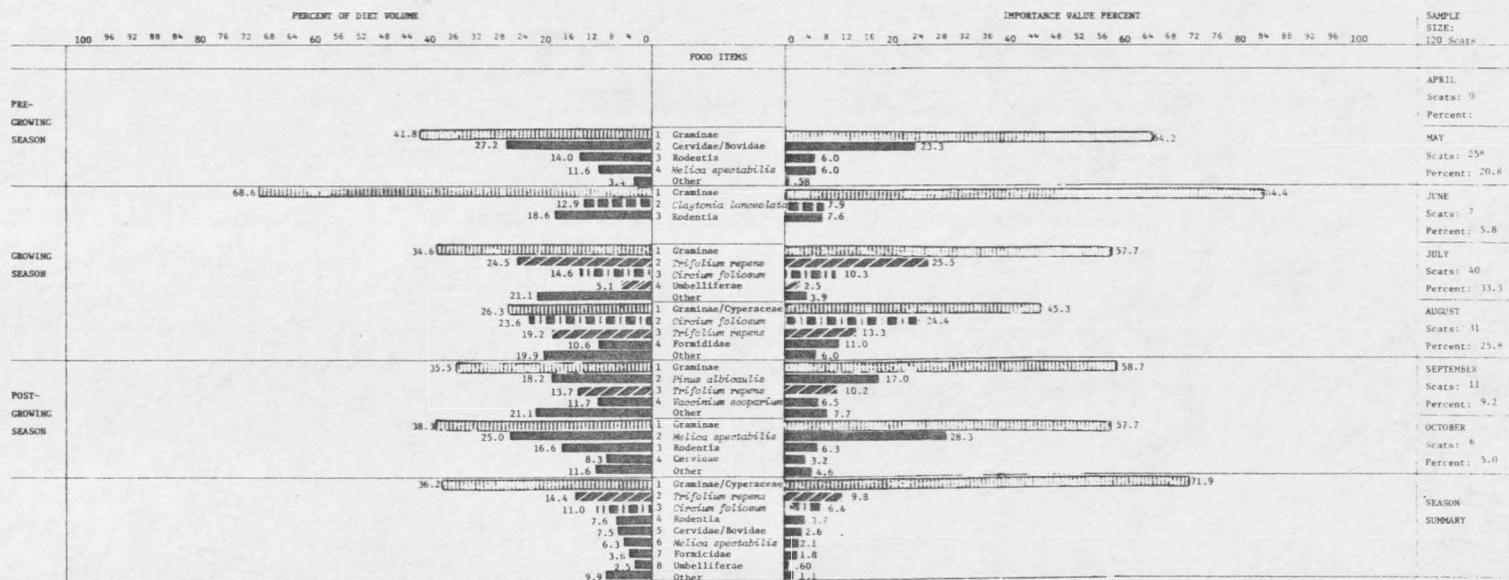
Table 2 and Figure 7 show, with one exception, seasonal food item consumption in 1973. The May sample was collected between 1968 and 1973 at the rate of 4-5 scats per year. Grasses and sedges greatly exceeded all other food items in importance in all months (Table 2). Animal material and corms of melica grass (*Melica spectabilis*) were most important as foods during the pre- and post-growing seasons (Figure 7). In Table 3, the annual summary, the percent compositions per item of the six highest ranking foods are near or above fifty percent indicating that these items were specifically selected.

Table 4 and Figure 8 show seasonal food item consumption in 1974. They indicate that grasses and sedges were the most important foods in all months except April when artiodactyls were most important. Grass



Photo by Mary Meagher

Figure 6. Hayden Valley and associated lodgepole pine forest: an example of a valley/plateau economy setting.



*Scats from previous years.

Figure 7. Grizzly bear seasonal food consumption in Yellowstone National Park - valley/plateau economy, 1973.

TABLE 3. YELLOWSTONE NATIONAL PARK VALLEY/PLATEAU ECONOMY GRIZZLY BEAR FOOD CONSUMPTION SUMMARY, 1973.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
Graminae/Cyperaceae	Graminae 94% Stems Leaves						
	<i>Carex</i> sp. 6% Heads	7767	70.8	51.1	36.20	25.600	71.900
<i>Trifolium repens</i>	Stems/Leaves/Heads	7590	24.2	59.5	14.40	3.500	9.800
<i>Cirsium foliosum</i>	Stems/Heads	7476	20.8	52.6	11.00	2.300	6.400
Rodentia	<i>Thomomys talpoides</i> 52% <i>Microtus</i> 48%	7524	17.5	43.4	7.60	1.300	3.700
Cervidae/Bovidae	<i>Cervus canadensis</i> 88% <i>Odocoileus hemionus</i> 6% <i>Bison bison</i> 6%	7257	12.5	59.7	7.50	.940	2.600
<i>Melica spectabilis</i>	Corns	7829	11.7	53.7	6.30	.740	2.100
Formicidae	Mature/Larvae	7935	16.7	23.0	3.80	.630	1.800
Umbelliferae	<i>Perideridia gairdneri</i> 70% - Roots <i>Lomatium cous</i> 30% - Roots	7130	8.3	30.5	2.50	.210	.600
<i>Equisetum arvense</i>	Stems	8217	5.0	42.5	2.10	.110	.310
<i>Polygonum bistortoides</i>	Entire	7811	7.5	17.2	1.30	.100	.280
<i>Pinus albicaulis</i>	Nuts	7880	4.2	40.0	1.70	.070	.200
<i>Claytonia lanceolata</i>	Entire	7962	3.3	47.5	1.60	.050	.140
<i>Vaccinium scoparium</i>	Berries/Leaves	7900	3.3	34.5	1.20	.040	.110
Garbage		7800	1.6	60.0	1.00	.020	.060
<i>Heracleum lanatum</i>	Stems/Leaves	8125	1.6	37.5	.60	.010	.020
Vespidae	Mature/Larvae	7600	1.6	18.2	.30	.005	.010
<i>Ranunculus</i> sp.	Stems/Leaves/Flowers	8200	.8	10.0	.08	.001	.003
		Avg. 7683			89.18	35.626	100.043

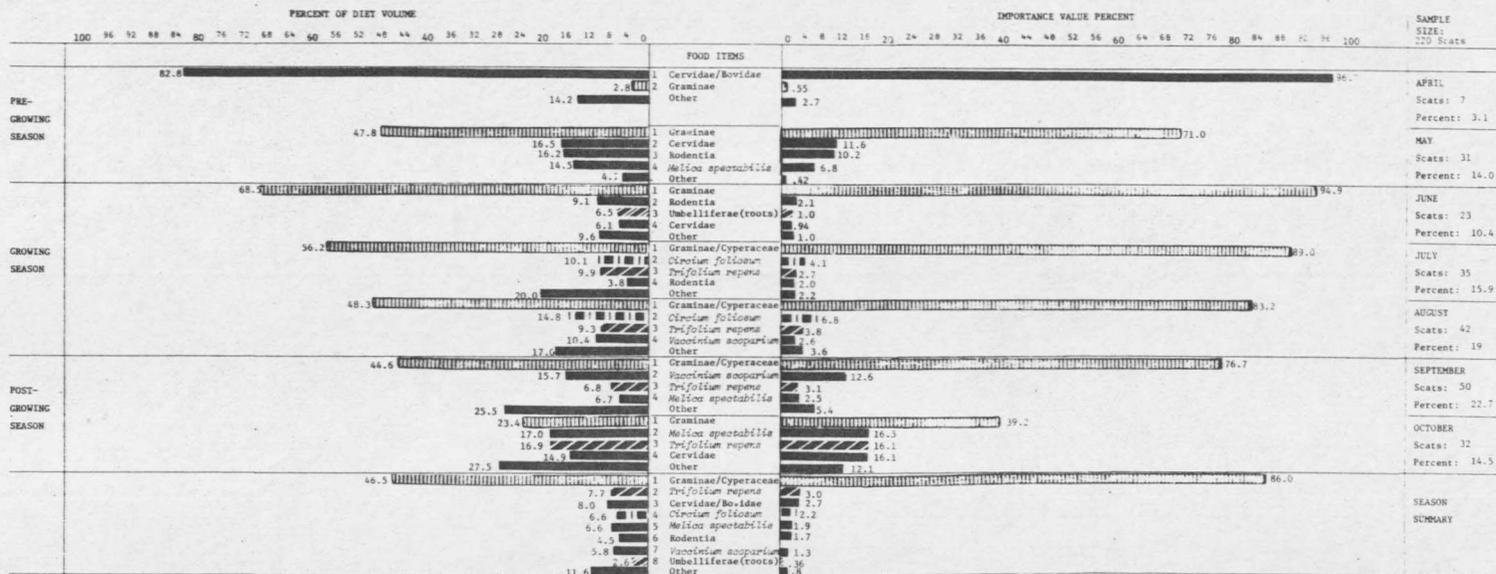


Figure 8. Grizzly bear seasonal food consumption in Yellowstone National Park - valley/plateau economy, 1974.

was most important in June and least important in October. Non-grass items including, notably, artiodactyls and melica corms were most important during the pre- and post-growing seasons (Figure 8). Low red huckleberries (*Vaccinium scoparium*), strawberries (*Fragaria virginiana*), and pine nuts (*Pinus albicaulis*) contributed to the diet during the late growing season and post-growing season.

In Table 4, the rank order of food items listed for May 1974 is identical with those of the May 1968-73 sample shown in Table 2. The importance value percents are comparable.

In the annual summary (Table 5), the Percent Composition Per Item column shows high selectivity for the more important foods as well as for some less important.

Table 6 and Figure 9 compare 1973 and 1974 valley/plateau economy data. The diets each year were similar. Grasses and sedges were the most important item both years. Substantial differences exist between the years in the importance value percents of white clover (*Trifolium repens*), and elk thistle (*Cirsium foliosum*). These differences exist because an area with scats containing primarily the remains of these items was sampled in 1973, but not in 1974. The average elevations of scat location are nearly identical for the two years. Table 7 and Figure 9 show two-year summaries of results. They indicate that grasses and sedges constituted 82 percent of diet importance and 42.9

TABLE 5. YELLOWSTONE NATIONAL PARK VALLEY/PLATEAU ECONOMY GRIZZLY BEAR FOOD CONSUMPTION SUMMARY, 1974.

Food Item	Use	Elevation	Frequency	Percent	Percent	Importance	Importance
			Occurrence	Composition	of Diet		
			Percent	Per Item	Volume		Percent
Graminae/Cyperaceae	Graminae 97%						
	Stems						
	Leaves						
	Carex sp. 3%	7620	67.7	68.7	46.50	31.5000	86.000
Trifolium repens	Stems/Leaves/Heads	7906	14.1	54.3	7.70	1.1000	3.000
Cervidae/Bovidae	Cervus canadensis 89%						
	Odocoileus hemionus 7%						
	Bison bison 4%	7595	12.3	65.4	8.00	.9900	2.700
Cirsium foliosum	Stems/Heads	7858	12.3	53.8	6.60	.8100	2.200
Melica spectabilis	Corms	7590	10.4	63.2	6.60	.6800	1.200
Rodentia	Thomomys talpoides 63.3%						
	Microtus 33.3%						
	Marmota flaviventris 3.3%	7595	13.6	32.8	4.50	.6100	1.700
Vaccinium scoparium	Berries/Leaves	7863	8.6	66.8	5.20	.4900	1.300
Umbelliferae	Perideridia gairdneri 73% - Roots						
	Lomatium cous 27% - Roots	7458	5.0	52.5	2.60	.1300	.360
Russula sp.	Caps/Stems	7935	5.9	25.4	1.50	.0900	.240
Polygonium bistortoides	Entire	7807	4.5	22.5	1.00	.0500	.120
Formicidae	Mature/Larvae	7554	5.4	15.5	.83	.0400	.120
Taraxicum sp.	Stems/Heads/Leaves	7960	2.3	54.0	1.20	.0300	.080
Pinus albicaulis	Nuts	7900	2.2	59.0	1.30	.0300	.080
Smilacina sp.	Rhizomes	8028	1.8	71.3	1.30	.0200	.060
Garbage		7778	1.3	76.6	1.00	.0100	.040
Agoseris sp.	Stems/Leaves/Heads	7038	.90	97.5	.88	.0060	.020
Forb - U/I	Stems	7050	.90	75.0	.87	.0060	.020
Fragaria virginiana	Fruits	7846	1.8	17.5	.31	.0050	.010
Equisetum arvense	Stems	7885	.90	47.5	.42	.0040	.010
Aster integrifolius	Stems/Leaves	7800	.45	95.0	.43	.0020	.010
Angelica sp.	Stems/Leaves	7900	.90	27.5	.24	.0020	.010
Chlorophyceae	Entire	6800	.45	50.0	.23	.0010	.003
Ranunculus sp.	Stems/Leaves/Heads	7870	.45	30.0	.14	.0006	.002
Vespidae	Mature/Larvae	7800	.90	10.0	.09	.0008	.002
	Avg.	7687			99.84	36.6074	99.987

TABLE 6. YELLOWSTONE NATIONAL PARK VALLEY/PLATEAU ECONOMY GRIZZLY BEAR KEY FOOD ITEM CONSUMPTION COMPARISON, 1973-1974.

1973				1974			
Scat Sample - 120				Scat Sample - 220			
Food Item	Importance	Percent	Average	Food Item	Importance	Percent	Average
	Value	Total	Ele-		Value	Total	Ele-
	Percent	Value	vation		Percent	Value	vation
Graminae/ Cyperaceae	71.9			Graminae/ Cyperaceae	86.0		
<i>Trifolium</i> <i>repens</i>	9.8			<i>Trifolium</i> <i>repens</i>	3.0		
<i>Cirsium</i> <i>foliosum</i>	6.4			Cervidae/ Bovidae	2.7		
Rodentia	3.7			<i>Cirsium</i> <i>foliosum</i>	2.2		
Cervidae/ Bovidae	2.6			<i>Melica</i> <i>spectabilis</i> (Corms)	1.9		
<i>Melica</i> <i>spectabilis</i> (Corms)	2.1			Rodentia	1.7		
Formicidae	1.8			<i>Vaccinium</i> <i>scoparium</i>	1.3		
		98.3	7683			98.8	7687

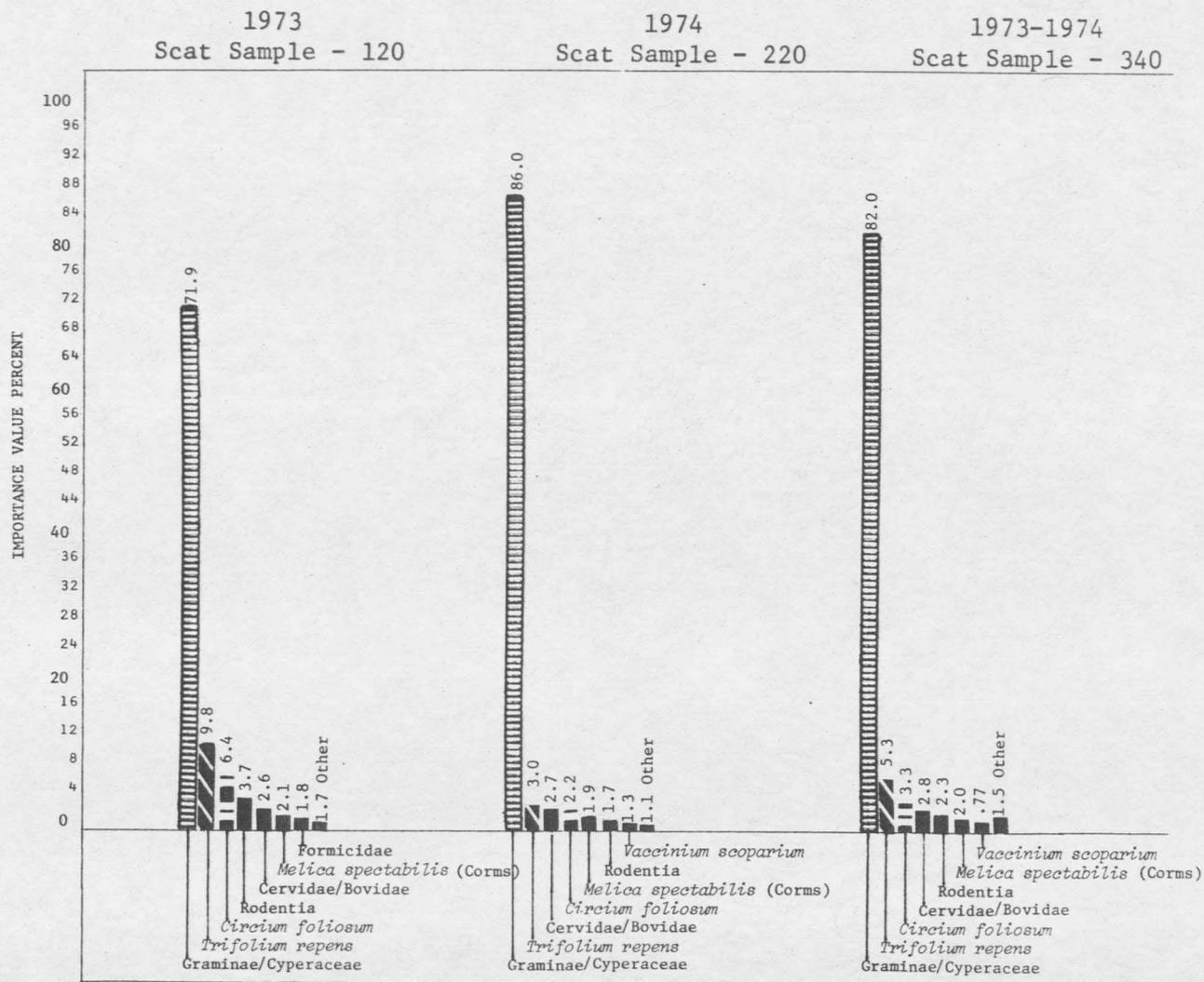


Figure 9. Yellowstone National Park valley/plateau economy grizzly bear key food item consumption comparison and summary, 1973-1974.

TABLE 7. YELLOWSTONE NATIONAL PARK VALLEY/PLATEAU ECONOMY GRIZZLY BEAR FOOD CONSUMPTION
SUMMARY, 1973-1974.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
Graminae/Cyperaceae	Graminae 96% Stems Leaves						
	<i>Carex</i> sp. 4% Heads	7673	68.8	62.3	48.80	29.5000	82.000
<i>Trifolium repens</i>	Stems/Leaves/Heads	7753	17.6	63.0	11.10	1.9000	5.300
<i>Cirsium foliosum</i>	Stems/Heads	7674	15.3	53.2	8.10	1.2000	3.300
Cervidae/Bovidae	<i>Cervus canadensis</i> 88% <i>Odocoileus hemionus</i> 7% <i>Bison bison</i> 5%	7474	12.4	63.4	7.80	1.0000	2.800
Rodentia	<i>Thomomys talpoides</i> 59% <i>Microtus</i> 39% <i>Marmota flaviventris</i> 2%	7566	15.0	37.2	5.80	.8400	2.300
<i>Melica spectabilis</i>	Corms	7680	10.9	59.6	8.80	.7100	2.000
<i>Vaccinium scoparium</i>	Berries/Leaves	7869	6.8	61.2	4.10	.2800	.770
Formicidae	Mature/Larvae	7875	9.4	20.2	1.80	.1800	.500
Umbelliferae	<i>Perideridia gairdneri</i> 71% - Roots <i>Lomatium cous</i> 29% - Roots	7302	6.2	42.0	2.80	.1600	.440
<i>Polygonum bistortoides</i>	Entire	7809	5.6	20.0	1.10	.0600	.170
<i>Russula</i> sp.	Caps/Stems	7935	3.8	25.4	.87	.0400	.100
<i>Pinus albicaulis</i>	Nuts	7890	3.0	49.5	1.80	.0400	.100
<i>Equisetum arvense</i>	Stems	7968	2.4	43.8	1.00	.0200	.050
Garbage		7787	1.5	70.0	1.00	.0200	.040
<i>Taraxacum</i> sp.	Stems/Leaves/Heads	7960	1.5	54.0	.80	.0100	.030
<i>Claytonia lanceolata</i>	Entire	7962	1.2	47.5	.88	.0070	.020
<i>Agoseris</i> sp.	Stems/Leaves/Heads	7038	.60	97.5	.87	.0030	.008
Forb - U/I	Stems/Leaves	7050	.60	75.0	.44	.0030	.008
<i>Fragaria virginiana</i>	Fruits	7846	1.2	17.5	.81	.0030	.008
Vespidae	Mature/Larvae	7700	1.2	14.1	.17	.0020	.006
<i>Heraclium lanatum</i>	Stems/Leaves	8125	.60	37.5	.82	.0010	.003
<i>Angelica</i> sp.	Stems/Leaves	7900	.60	27.5	.18	.0010	.003
<i>Aster integrifolius</i>	Stems/Leaves	7800	.30	100.0	.88	.0009	.003
<i>Ranunculus</i> sp.	Stems/Leaves/Flowers	8035	.60	20.0	.18	.0007	.002
Chlorophyceae	Entire	6800	.30	50.0	.18	.0004	.001
		Avg. 7685			99.86	35.9820	99.962

percent of diet volume. Percent composition per item for grasses and sedges is 62.3 percent suggesting that feeding was selective for these items.

The general feeding cycle appeared to follow plant phenology. During the pre-growing season, grizzlies were primarily meat eaters. They apparently congregated on ruminant wintering areas and took the animal material available. Cole (1972) has detailed this activity. In addition, corms, roots, and grass were eaten prior to and during early green-up. During the growing season, grasses, sedges, forbs and rodents were used almost exclusively as food. Field observations indicated that succulent vegetation was preferred and its availability, linked with that of rodents, apparently influenced distribution. Since most plants were generally succulent at this time, bear distribution appeared to be wide and open areas were feeding sites. During the post-growing season, grasses and forbs remained important foods, but their use seemed to be confined to moist sites usually in small forest openings and edges and stream bottoms. Seasonal foods in the lodgepole pine forests became available as grasses, sedges and forbs in the valleys desiccated; nuts and berries were taken along with mushrooms (*Russula* sp.) and the rhizomes of smilacina (*Smilacina* sp.). Field observations also indicated that predation on adult, male, breeding elk (*Cervus canadensis nelsoni*) may also have occurred. Extensive use was made of melica corms in

Pelican and Lamar Valleys. Distribution appeared to be concentrated in local areas throughout the economy.

Intensive digging was the characteristic feeding activity of valley/plateau economy grizzlies, especially during the growing season. The presence of pocket gophers (*Thomomys talpoides*) and voles (*Microtus* sp.) apparently motivated this activity. Field observations showed that locally concentrated excavations ranged in volume from a few hundred cm.³ to nearly a hundred m.³. Most were from 1-5 m.³ in volume. Large numbers of scats were often found associated with digging sites. Contents of these scats averaged 90 percent residues of grasses and forbs and 10 percent residues of rodents. All evidence suggests that these grizzlies pursued meat (rodents) but settled for grasses and forbs and a small amount of meat. The small, but consistent amount of success in catching rodents probably held the bears in the feeding pattern. Murie (1961) noted a similar pattern among grizzlies in Mt. McKinley National Park where bears pursued rodents with marginal success for several hours, and then with resignation, finished the feeding period grazing on grass. After resting, the cycle was repeated. Intensive digging activity and associated evidence of grazing usually occurred in locations where xeric sites were interspersed with mesic sites. The excavations occurred on the xeric sites while grazing occurred on the adjacent mesic sites.

The intensive digging pattern is illustrated by an incident which occurred in July 1974 in Hayden Valley. On July 11, near lower Alum Creek, I found an area of approximately 5,000 m.² which had the appearance of a freshly ploughed field. Twenty grizzly scats containing primarily the residues of grasses and sedges and a trace of rodent remains were located immediately below the site near a small watercourse. The apparent incongruity between digging effort and food eaten was confusing. I returned to the digging site three days later with my dog. The leashed dog's reaction was remarkable. In a frenzied state he pulled free and immediately caught three voles. The sight, sound and smell of voles were the apparent causes for the dog's reaction. The grizzly reaction to the locally high population of voles may have been similar and resulted in a kind of "overkill" excavation effort. Ultimately, the main food taken was succulent grass. The presence of voles appeared to anchor the bear(s) to the area.

Another link between rodent activity and plant food became apparent early in October 1973 while observing two adolescent grizzlies feeding in Pelican Valley. The bears appeared to travel a random course sniffing the ground intently. They would stop occasionally and dig furiously for a few moments and then feed. Inspection of the feeding sites revealed that the bears were locating, digging out and eating the contents of pocket gopher nests. All of these nests

contained caches of roots, bulbs and corms. One-half kg., dry weight, of these items remained at a nest site where a bear had fed.

Field observations suggested that white clover was the most highly preferred and highly selected plant food eaten during the growing season. Where it was abundant, especially along upper Pelican Creek and in thermal areas between Mary Lake and Hayden Valley, it was used extensively. As many as 50 scats containing exclusively white clover residues were found in individual white clover patches. This item also appeared to be preferred by elk and bison (*Bison bison*) and was heavily used by them in September. Such use often removed white clover from grizzlies as a significant food source.

The relationship between grizzly distribution and plant succulence was most apparent in the Pelican Valley-Fishing Bridge area. During the early and middle portion of the growing season, vegetation was generally succulent throughout the area and bears seemed widely distributed. The only concentrated feeding activity occurred in white clover patches and in areas with high rodent densities. During the late growing season and post-growing season, all herbaceous vegetation except that on moist sites became desiccated and grizzly feeding was confined to the moist sites. The largest proportion of moist sites seemed to occur in small openings which were interspersed throughout the lodgepole pine forest in lower Pelican Valley and near the Fishing Bridge Campground. Grizzlies appeared to be drawn to these moist sites

with their remaining succulent grasses and forbs. The most dramatic evidence of this effect was observed on October 2, 1974 at the Fishing Bridge sewage lagoons. On this date, bluegrass (*Poa* sp.), brome (*Bromus* sp.) and other grasses remained succulent on the lagoon dikes near the sludge. All other herbaceous vegetation in the vicinity and in the Park generally appeared brown. Intense grazing on the dikes by grizzlies was evident. Feeding was particularly intense on the banks where grass removal had exposed mineral soil. Sixty-five fresh scats were counted in the area.

A different pattern of post-growing season food use was revealed by an incident which occurred in the western extreme of Hayden Valley on October 4, 1974. During the night my camp at Mary Lake Patrol Cabin was visited by a grizzly. Tracks in the snow indicated that the bear had shared grain pellets with my tied horses. It then left the camp. Soon after daylight I followed the tracks on horseback. As it traveled, the bear had fed on mushrooms and the rhizomes of smilacina. Since there was no moon, the bear probably detected the presence of these items by smell. The trail led through some thermal areas where the bear had eaten white clover. I tracked the bear to the edge of Hayden Valley where it was unintentionally encountered at short range feeding on the putrid carcass of a bull elk. On October 10, I revisited the location and found only the broken skull and 7-point antlers of the elk. Tooth wear indicated the elk had been 7-9 years old. The

general appearance of the site suggested that the elk had been killed.

This incident is probable evidence that some grizzlies become predatory on vulnerable ruminants, in this case probably an unwary breeding bull, during the post-growing season after herbs have dried. The result of this successful predation, the possession of an elk carcass, did not appear to have precluded other foraging activities. Most scats collected near the elk cache contained mixtures of residues of plant and elk origin.

Mountain Economy

The Gallatin (Figure 10) and Washburn Ranges were major centers of the mountain economy. The fertile andesitic and sedimentary derived soils of the economy supported abundant vegetation in mountain meadows and parklands and on ridgetops. These sites provided most of the food items in the economy.

Table 8 and Figure 11 show seasonal food consumption in 1973. Western springbeauty (*Claytonia lanceolata*) was the most important food during the growing season months. Grasses ranked a distant second. Grasses and pine nuts were the most important foods during the post-growing season. Table 9, the annual summary, shows that springbeauty and pine nuts were highly selected as indicated by their respective percent compositions per item.



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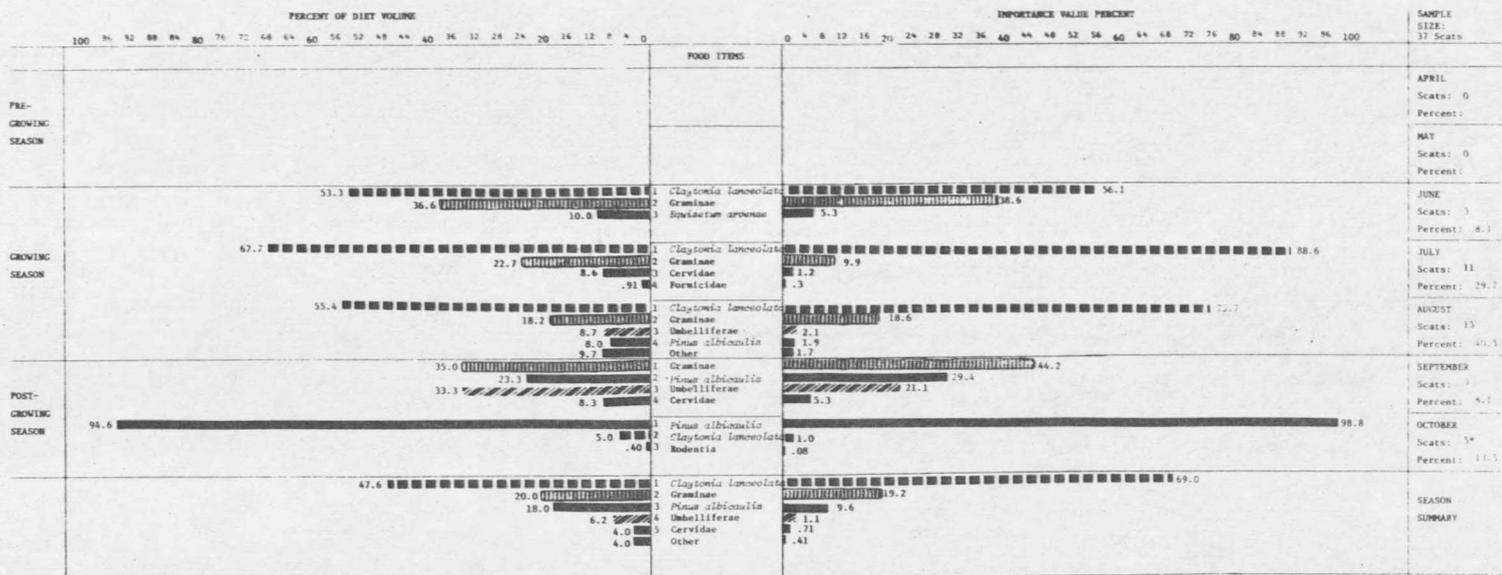
Photo by Jim Chester

Figure 10. Gallatin Mountains with Joseph Peak to the left and Electric Peak to the right: an example of a mountain economy setting.

TABLE 8. GRIZZLY BEAR SEASONAL FOOD CONSUMPTION IN YELLOWSTONE NATIONAL PARK -
MOUNTAIN ECONOMY, 1973.

Month	Sample	Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent		
June	3	<i>Claytonia lanceolata</i>	Entire	8000	66.6	80.0	53.3	35.5	58.1		
		Graminae	Stems/Leaves/Heads	8650	66.6	55.0	36.6	24.4	38.6		
		<i>Equisetum arvense</i>	Stems	7500	33.3	30.0	10.0	3.3	5.3		
		Avg.	8160				99.9	63.2	100.0		
July	11	<i>Claytonia lanceolata</i>	Entire	9000	81.8	82.8	67.70	55.40	88.6		
		Graminae	Stems/Leaves/Heads	8700	27.3	83.3	22.70	6.20	9.9		
		Cervidae	<i>Cervus canadensis</i>	9100	9.0	95.0	8.60	.77	1.2		
		Formicidae	Mature/Larvae	8850	18.2	5.0	.91	.17	.3		
		Avg.	8927				99.91	62.54	100.0		
August	15	<i>Claytonia lanceolata</i>	Entire	9150	80.0	69.2	55.40	44.30	75.70		
		Graminae	Stems/Leaves/Heads	8888	60.0	30.3	18.20	10.90	18.00		
		Umbelliferae	<i>Lomatium cous</i> - Roots	9500	13.3	65.0	8.70	1.20	2.10		
		<i>Pinus albicaulis</i>	Nuts	9250	13.3	60.0	8.00	1.10	1.90		
		<i>Russula</i> sp.	Cap/Stem	8450	13.3	30.0	4.00	.53	.90		
		<i>Vaccinium scoparium</i>	Berries/Leaves	8800	6.6	40.0	2.60	.17	.29		
		Formicidae	Mature/Larvae	9400	20.0	4.0	.80	.16	.27		
		Cervidae	<i>Cervus canadensis</i>	7600	6.6	25.0	1.65	.11	.19		
		<i>Circium foliosum</i>	Stems	9300	6.6	10.0	.66	.04	.07		
		Avg.	9056				100.01	58.51	100.02		
		September	3	Graminae	Stems/Leaves/Heads	8300	66.6	52.5	35.0	23.3	44.2
<i>Pinus albicaulis</i>	Nuts			8300	66.6	35.0	23.3	15.5	29.4		
Umbelliferae	<i>Lomatium cous</i> - Roots			9100	33.3	100.0	33.3	11.1	21.1		
Cervidae	<i>Cervus canadensis</i>			9000	33.3	25.0	8.3	2.8	5.3		
Avg.	8550						99.9	52.7	100.0		
October	5*	<i>Pinus albicaulis</i>	Nuts	8900	100.0	94.6	94.6	94.60	98.80		
		<i>Claytonia lanceolata</i>	Entire	8600	20.0	25.0	5.0	1.00	1.00		
		Rodentia	<i>Microtus</i>	8800	20.0	2.0	.4	.08	.08		
Total Sample	37			Avg.	8843				100.0	95.68	99.88

*Scats from previous years.



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*Scats from previous year.

Figure 11. Grizzly bear seasonal food consumption in Yellowstone National Park - mountain economy, 1973.

TABLE 9. YELLOWSTONE NATIONAL PARK MOUNTAIN ECONOMY GRIZZLY BEAR FOOD CONSUMPTION SUMMARY, 1973.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
<i>Claytonia lanceolata</i>	Entire	8975	65.0	73.4	47.60	30.900	69.000
Graminae	Stems/Leaves/Heads	8750	43.2	46.1	20.00	8.600	19.200
<i>Pinus albicaulis</i>	Nuts	8844	24.0	73.6	18.00	4.300	9.600
Umbelliferae	<i>Lomatium cous</i> - Roots	9367	8.1	77.0	6.20	.500	1.100
Cervidae	<i>Cervus canadensis</i>	8567	8.1	48.3	4.00	.320	.710
<i>Cirsium foliosum</i>	Stems/Heads	9300	8.1	10.0	.80	.060	.130
Formicidae	Mature/Larvae	9125	10.8	4.5	.50	.050	.110
<i>Vaccinium scoparium</i>	Berries/Leaves	8800	2.7	40.0	1.10	.030	.070
<i>Fussula</i> sp.	Caps/Stems	8450	2.7	30.0	.81	.020	.050
<i>Equisetum arvense</i>	Stems	7500	2.7	30.0	.81	.020	.050
Rodentia	<i>Microtus</i>	8800	2.7	2.0	.05	.001	.002
	Avg.	8890			99.87	44.801	100.022

Tables 10, 11, and Figure 12 show 1974 food consumption. Springbeauty and grasses were the most important food items in June, July and August. Springbeauty was the most important item in July and was of nearly equal importance with grasses in August. In September, grasses and sedges were most important. Scats containing the remains of these items were found at an average elevation of 8330 feet (2539 m.). Pine nuts ranked second and scats containing pine nut residues were found at an average elevation close to that of scats containing grass/sedge residues. Percent compositions per item of these two foods indicate that they were taken in combination with other items (Table 10). Most scats containing pine nut residues also contained grass residues. In October, pine nuts were the most important item and scats containing pine nut residues were found at an average elevation of 9200 feet (2804 m.). This item was exclusively selected (Table 10).

Table 12 and Figure 13 compare 1973 and 1974 mountain economy data. The most important food items consumed each year were identical, their contributions to total diet importance were nearly identical and their rank orders are similar. Springbeauty ranked first, and grasses and sedges ranked second each year. Large differences in importance values for the different food items exist between years. These differences are the probable result of incomplete and sporadic sampling in 1973 as compared with that of 1974. The average

TABLE 10. GRIZZLY BEAR SEASONAL FOOD CONSUMPTION IN YELLOWSTONE NATIONAL PARK - MOUNTAIN ECONOMY, 1974.

Month	Sample	Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent		
June	4	Graminae	Stems/Leaves	8853	75.0	46.6	34.9	26.2	61.5		
		<i>Equisetum arvense</i>	Stems	8200	25.0	100.0	25.0	6.3	14.8		
		Umbelliferae	<i>Perideridia gairdneri</i> - Roots	8360	25.0	60.0	15.0	3.8	8.9		
		<i>Trifolium repens</i>	Stems/Leaves	8800	25.0	50.0	12.5	3.1	7.3		
		Cervidae	<i>Cervus canadensis</i>	9400	25.0	30.0	7.5	1.9	4.5		
		Rodentia	<i>Thomomys talpoides</i>	8360	25.0	20.0	5.0	1.3	3.1		
			Avg.			8710			99.9	42.6	100.1
July	52	<i>Claytonia lanceolata</i>	Entire	9456	59.6	83.5	49.80	29.70	61.80		
		Graminae	Stems/Leaves	9210	48.0	63.0	30.30	14.50	30.20		
		Umbelliferae	<i>Lomatium couis</i> 71% - Roots								
			<i>Perideridia gairdneri</i> 29% - Roots	9286	27.0	49.6	13.40	3.60	7.50		
		Rodentia	<i>Thomomys talpoides</i>	9450	3.8	52.5	2.00	.08	.17		
		Formicidae	Mature/Larvae	9380	9.6	7.2	.69	.06	.13		
		Chlorophyceae	Entire	8000	1.9	100.0	1.90	.04	.08		
		<i>Equisetum arvense</i>	Stems	8400	1.9	100.0	1.90	.04	.08		
			Avg.			9311			99.99	48.02	99.96
August	60	Graminae/Cyperaceae	Graminae 79% Stems Leaves								
			<i>Carex</i> sp. 21% Heads	8666	71.6	43.0	30.80	22.000	47.300		
		<i>Claytonia lanceolata</i>	Entire	9590	50.0	87.6	43.80	21.900	47.000		
		Umbelliferae	<i>Lomatium couis</i> 82% - Roots								
			<i>Perideridia gairdneri</i> 18% - Roots	9141	18.3	35.4	6.50	1.200	2.600		
		<i>Heracleum lanatum</i>	Stems/Leaves	8500	11.6	44.0	5.10	.600	1.300		
		Formicidae	Mature/Larvae	8981	13.3	22.7	3.00	.400	.860		
		<i>Circium foliosum</i>	Stems/Leaves/Heads	8975	6.6	50.0	3.30	.220	.470		
		<i>Trifolium repens</i>	Stems/Leaves/Heads	7750	6.6	22.5	1.50	.100	.220		
		<i>Mertensia ciliata</i>	Stems/Leaves	9325	3.3	50.0	1.60	.050	.100		
		<i>Pinus albicaulis</i>	Nuts	8200	5.0	13.3	.87	.030	.060		
		<i>Equisetum arvense</i>	Stems	8000	1.6	90.0	1.40	.020	.040		
		<i>Ranunculus</i> sp.	Stems/Leaves/Flowers	7600	1.6	50.0	.80	.010	.020		
		<i>Pastinaca sativa</i>	Stems/Leaves	8900	1.6	50.0	.80	.010	.020		
		Rodentia	<i>Thomomys talpoides</i>	9000	1.6	25.0	.40	.006	.010		
		<i>Fragaria virginiana</i>	Fruits	8500	1.6	20.0	.32	.005	.010		
		<i>Russula</i> sp.	Caps/Stems	8000	1.6	10.0	.16	.002	.004		
			Avg.			8849			100.15	46.553	100.014
		September	13	Graminae/Cyperaceae	Graminae 86% Stems Leaves						
					<i>Carex</i> sp. 14% Heads	8330	53.8	49.9	26.8	14.40	42.4
				<i>Pinus albicaulis</i>	Nuts	8405	46.1	35.8	16.5	7.60	22.4
<i>Claytonia lanceolata</i>	Entire			8175	30.7	63.7	19.6	6.00	17.7		
<i>Ribes setosum</i>	Berries/Leaves			8600	15.3	100.0	15.3	2.30	6.8		
Rodentia	<i>Thomomys talpoides</i>			8420	15.3	65.0	10.0	1.50	4.4		
<i>Fragaria virginiana</i>	Fruits			8300	23.0	23.3	5.4	1.20	3.5		
Umbelliferae	<i>Lomatium couis</i> - Roots			8120	15.3	40.0	6.1	.93	2.7		
	Avg.					8336			99.7	33.93	99.9
October	4	<i>Pinus albicaulis</i>	Nuts	9200	74.0	100.0	75.0	55.5	89.6		
		Umbelliferae	<i>Lomatium couis</i> - Roots	9233	25.0	100.0	25.0	6.3	10.2		
			Avg.			9208			100.0	61.8	100.0
Total Sample	133										

TABLE 11. YELLOWSTONE NATIONAL PARK MOUNTAIN ECONOMY GRIZZLY BEAR FOOD CONSUMPTION SUMMARY, 1974.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
<i>Claytonia lanceolata</i>	Entire	9439	48.9	84.2	41.20	20.100	50.500
Graminae/Cyperaceae	Graminae 87% Stems Leaves						
	<i>Carex</i> sp. 13% Heads	8817	58.6	48.0	28.10	16.500	41.500
Umbelliferae	<i>Lomatium cous</i> 76% - Roots						
	<i>Perideridia gairdneri</i> 24% - Roots	9117	21.8	45.6	9.90	2.200	5.500
<i>Pinus albicaulis</i>	Nuts	8553	9.0	46.2	4.20	.380	.950
Formicidae	Mature/Larvae	9134	9.8	16.7	1.60	.160	.400
<i>Heraclium lanatum</i>	Stems/Leaves	8500	5.3	51.4	2.70	.140	.350
Rodentia	<i>Thomomys talpoides</i>	8850	4.5	46.7	2.10	.090	.220
<i>Equisetum arvense</i>	Stems	8200	2.2	96.6	2.20	.050	.130
<i>Cirsium foliosum</i>	Stems/Heads	8975	3.0	50.0	1.50	.050	.130
<i>Trifolium repens</i>	Stems/Leaves/Heads	7960	3.8	28.0	1.00	.040	.100
<i>Ribes setosum</i>	Berries/Leaves	8600	1.5	100.0	1.50	.020	.050
<i>Fragaria virginiana</i>	Fruits	8350	3.0	22.5	.68	.020	.050
<i>Mertensia ciliata</i>	Stems/Leaves	9325	1.5	50.0	.75	.010	.020
Chlorophyceae	Entire	8000	.75	100.0	.75	.006	.015
<i>Pastinaca sativa</i>	Stems/Leaves	8900	.75	50.0	.38	.003	.010
<i>Ranunculus</i> sp.	Stems/Leaves/Flowers	7600	.75	50.0	.38	.003	.010
Cervidae	<i>Cervus canadensis</i>	9400	.75	30.0	.23	.002	.005
	Avg.	8988			99.17	39.774	99.940

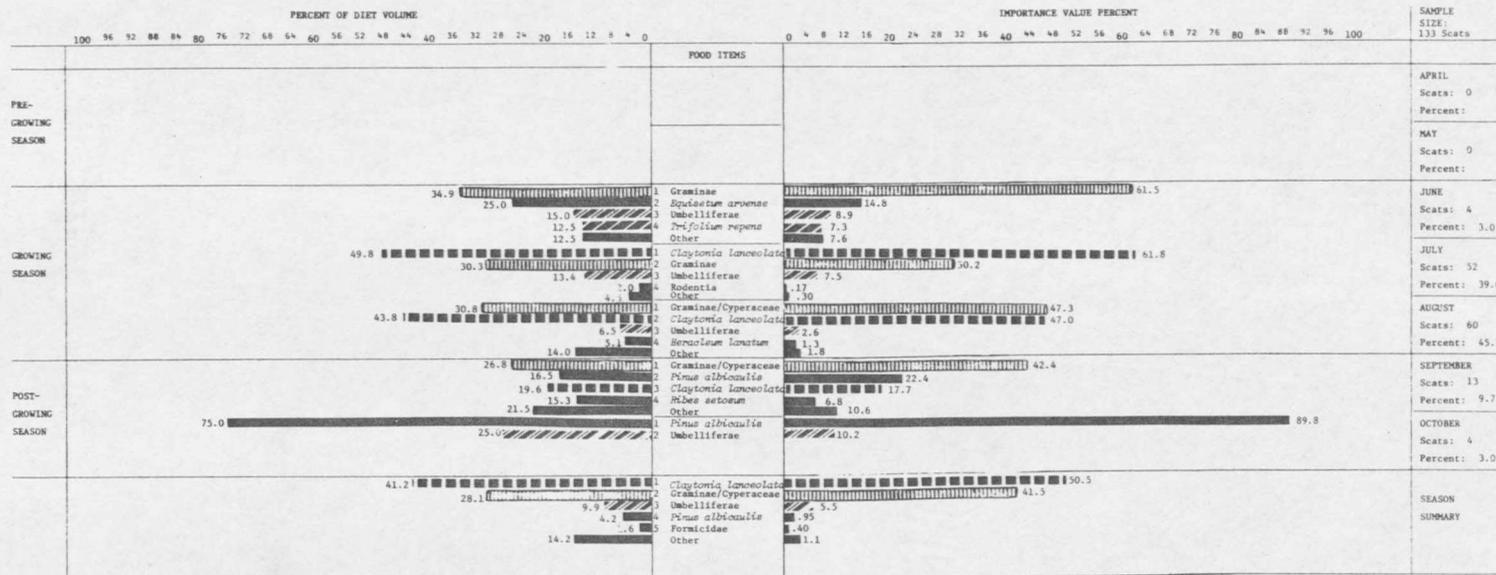


Figure 12. Grizzly bear seasonal food consumption in Yellowstone National Park - mountain economy, 1974.

TABLE 12. YELLOWSTONE NATIONAL PARK MOUNTAIN ECONOMY GRIZZLY BEAR KEY FOOD ITEM CONSUMPTION COMPARISON, 1973 - 1974.

Food Item	1973 Scat Sample - 37			1974 Scat Sample - 133		
	Importance Value Percent	Percent Total Importance Value	Average Ele- vation	Food Item	Importance Value Percent	Percent Total Importance Value
<i>Claytonia lanceolata</i>	69.0			<i>Claytonia lanceolata</i>	50.50	
Graminae/ Cyperaceae	19.2			Graminae/ Cyperaceae	41.50	
<i>Pinus albicaulis</i>	9.6			Umbelliferae (Roots)	5.50	
Umbelliferae (Roots)	1.1			<i>Pinus albicaulis</i>	.95	
		98.9	8890			98.45 8988

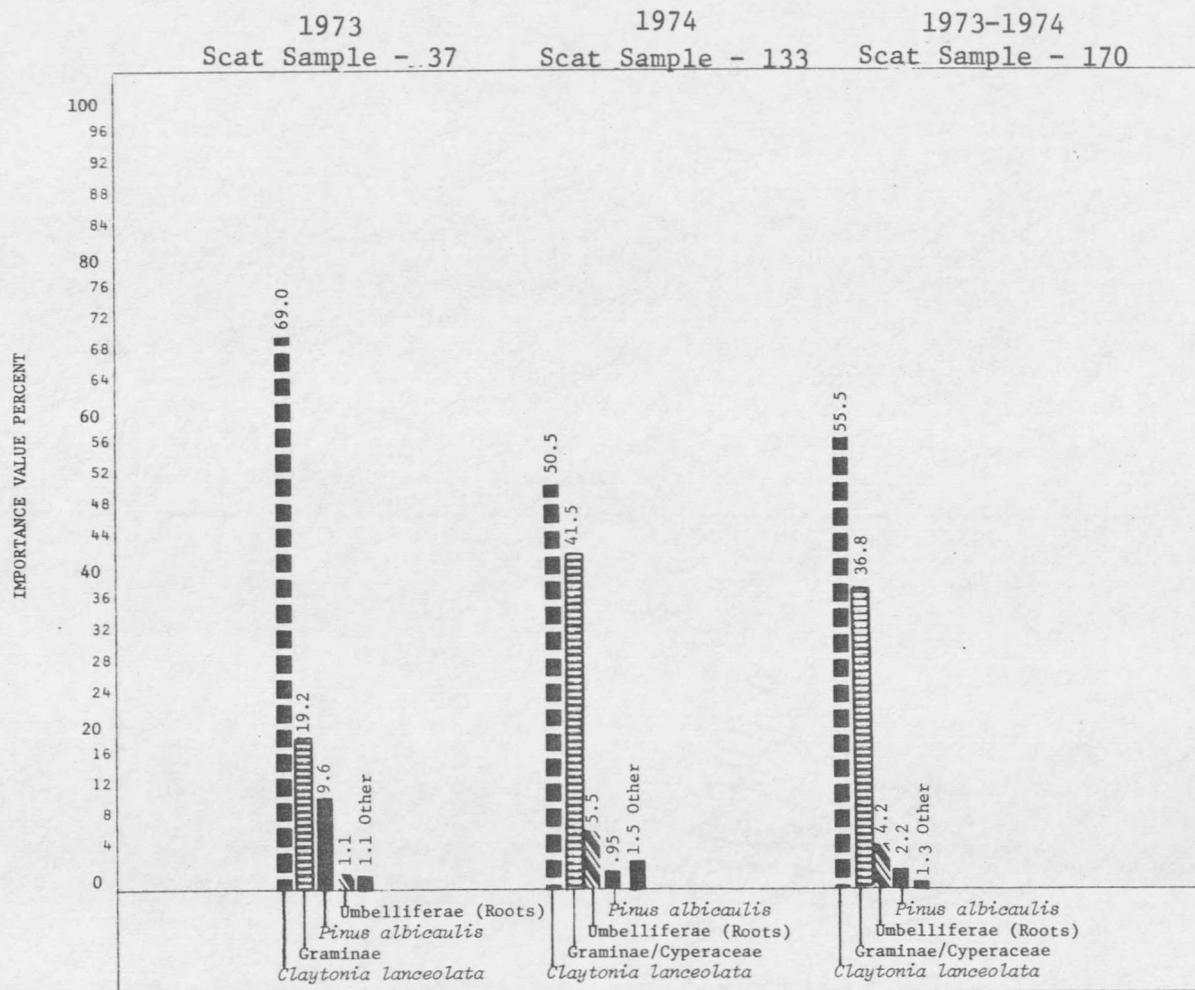


Figure 13. Yellowstone National Park mountain economy grizzly bear key food item consumption comparison and summary, 1973-1974.

elevations of scat location are comparable.

Table 13 and Figure 13, containing two-year summaries of results, show that springbeauty ranked first in food consumption importance with a value of 55.5 percent. Scats containing residues of this item were located at an average elevation of 9314 feet (2839 m.). Springbeauty was highly selected as indicated by the 81.3 percent composition per item. Grasses and sedges ranked second. These items were taken at an average elevation of 8806 feet (2684 m.). They were eaten in combination with other foods. The roots of Umbelliferae ranked third and were taken in combination with other items. Pine nuts ranked fourth. In September, they were taken below 2743 m. and eaten in combination with grass. In October, they were exclusively selected at elevations above 2743 m.

The general feeding cycle appeared to follow plant phenology as seemed to be the case for the valley/plateau economy. Elk and moose (*Alces alces shirasi*) wintering areas existed in the economy and use of ruminant material probably occurred during the pre-growing season although it was not sampled. During the growing season springbeauty and grasses and sedges were the most important foods. Field observations indicated that springbeauty was taken primarily in ridge-top herblands while grasses and sedges were taken in meadows and parklands. Feeding activities and distribution in relation to these foods appeared to be influenced by plant succulence. Feeding began

TABLE 13. YELLOWSTONE NATIONAL PARK MOUNTAIN ECONOMY GRIZZLY BEAR FOOD CONSUMPTION SUMMARY, 1973-1974.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
<i>Claytonia lanceolata</i>	Entire	9314	52.0	81.3	42.80	22.200	55.500
Graminae/Cyperaceae	Graminae 89% Stems Leaves						
	<i>Carex</i> sp. 11% Heads	8806	55.3	47.7	28.40	14.700	38.800
Umbelliferae	<i>Lomatium cous</i> 78% - Roots						
	<i>Perideridia gairdneri</i> 22% - Roots	9140	18.8	48.5	9.10	1.700	4.200
<i>Pinus albicaulis</i>	Nuts	8678	12.4	57.9	7.20	.900	2.200
Formicidae	Mature/Larvae	9132	10.0	13.8	1.40	.140	.360
<i>Heraclium lanatum</i>	Stems/Leaves	8550	4.1	51.4	2.10	.090	.220
Rodentia	<i>Thomomys talpoides</i> 86%						
	<i>Microtus</i> 14%	8843	4.1	40.3	1.70	.070	.170
<i>Cirsium foliosum</i>	Stems/Heads	9114	4.1	32.8	1.30	.050	.120
<i>Equisetum arvense</i>	Stems	8025	2.3	79.9	1.90	.040	.100
<i>Trifolium repens</i>	Stems/Leaves/Heads	7960	2.9	28.0	.82	.020	.050
Cervidae	<i>Cervus canadensis</i>	8775	2.3	43.7	1.00	.020	.050
<i>Ribes setosum</i>	Berries/Leaves	8600	1.2	100.0	1.20	.010	.020
<i>Fragaria virginiana</i>	Fruits	8350	2.3	22.5	.53	.010	.020
<i>Mertensia ciliata</i>	Stems/Leaves	9325	1.2	50.0	.58	.007	.018
Chlorophyceae	Entire	8000	.58	100.0	.58	.008	.008
<i>Pastinaca sativa</i>	Stems/Leaves	8900	.58	50.0	.29	.002	.005
<i>Ranunculus</i> sp.	Stems/Leaves/Flowers	7600	.58	50.0	.29	.002	.005
<i>Vaccinium scoparium</i>	Berries/Leaves	8800	.58	40.0	.23	.001	.003
<i>Russula</i> sp.	Caps/Stems	8450	.58	30.0	.17	.001	.003
	Avg.	8969			99.39	39.966	99.842

in snow-free locations and followed snow-melt and green-up to the highest elevations in late July and August (Table 10). 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. These sites were also attractive to elk and received intense grazing pressure from them. During the early post-growing season, feeding activities apparently continued to be influenced primarily by succulent vegetation associated with moist sites. Pine nuts and gooseberries (*Ribes setosum*) appeared to be eaten incidentally. In October following the desiccation of most herbs, feeding activity seemed to be concentrated on ridges generally above 2743 m. where pine nuts, Umbelliferae roots and springbeauty corms were taken exclusively.

Early post-growing season foraging of mountain economy grizzlies appeared similar to that of valley/plateau grizzlies in that both seemed to concentrate on moist sites with succulent herbs and use seasonal foods incidentally. Late post-growing season foraging appeared different in the two economies because mountain economy grizzlies ate nuts, roots and corms on high ridges while valley/plateau grizzlies fed on grasses, forbs, nuts, mushrooms, rhizomes, and ruminants in the lodgepole pine forest.

Casual digging was the characteristic feeding activity of mountain economy grizzlies. Field observations indicated that this digging was usually shallow and typically resulted in excavations having a volume of a few cm.³. The presence of springbeauty corms and biscuitroot (*Lomatium cous*) roots apparently motivated casual digging. A recount of the feeding activity of a large grizzly sow and yearling cub observed on August 25, 1974 at Fawn Pass in the Gallatin Range illustrated this activity. The bears were feeding in an open, rolling herbland of approximately 15 ha. They traveled slowly across the opening in an ambling gait which was interrupted by frequent stops to sniff and dig. The stops appeared to be random. No intense sniffing occurred until after the bears had stopped. After sniffing the ground, the bears overturned soil and plants with strong, purposeful scooping motions. Sometimes the animals appeared to feed on overturned material and at other times they seemed to ignore the dig and move on. Inspection of the dig sites revealed the remains of roots of biscuitroot and corms of springbeauty. Random digging in sites undisturbed by the bears yielded abundant amounts of these items. The above-ground portions of these plants were dried up and to me, scarcely recognizable. Earlier in the growing season, such casual digging probably would have been preceded by grazing on the above-ground parts of springbeauty.

Another observation of grizzly feeding activity one km. south of Big Horn Pass in the Gallatin Range on July 20, 1974 illustrates a variation of the casual digging pattern. The site was a rocky, alpine ridgetop. The bear was casually overturning rocks and earth with one paw. Each digging effort was followed by sniffing and eating. Inspection of the digs revealed that the bear was eating ants and roots of biscuitroot. General inspection of the entire 2 ha. feeding area revealed that it was literally terraced by past and present overturning of rocks and soil. Another site with an appearance similar to this one was located later, on Quadrant Mountain.

Grizzlies appeared to eat whitebark pine nuts in two distinct use stages: 1) incidental, and 2) exclusive. The incidental use stage occurred in late August and September when the mature cones remained in the trees. Mature cones in trees were unavailable to most grizzlies since all but the very young are unable to climb (Herrero, 1972). The only cones available during the incidental use stage were those on the ground as a result of squirrel (*Tamiasciurus hudsonicus*) cuts and wind throw. Since no direct link between grizzlies and cones existed during this stage, the primary foods were succulent forbs and grasses; pine nuts were eaten incidentally. This contrasted with black bear use during the same time. Black bears are adept climbers and I observed them ascending whitebark pine trees, breaking off cone-bearing limbs and descending to feed. Black bears separated the nuts from the cone

scales by holding the cone with the paws and tearing with the teeth. Only the nuts were ingested. The exclusive use stage occurred in October and probably November after cone disintegration and/or abscission. After abscission, nuts and cones became abundant on the ground and grizzlies were linked directly to them. A move to higher elevation ridges where whitebark pine is most abundant may have been a response to cone disintegration and abscission.

Grazing on grasses and sedges appeared to be 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 appeared to be grasped with the molars and plucked. Such feeding activity was performed rapidly and for long, uninterrupted periods.

Lake Economy

The primary components of the lake economy were spawning cutthroat trout (*Salmo clarki*), used as food by grizzlies, and the tributaries to Yellowstone Lake supporting spawning cutthroat trout (Figure 14). The economy functioned in the South, Southeast and Flat Mountain Arms of the Lake.

Table 14 and Figure 15 show growing season food consumption in 1973. Grass was the most important food in June and cutthroat trout was the most important food in July (Table 14). Other foods with



Photo by Dean Graham

Figure 14. Grizzly bear fishing in a tributary at the tip of the Flat Mountain Arm, Yellowstone Lake: an example of a lake economy setting.

TABLE 14. GRIZZLY BEAR SEASONAL FOOD CONSUMPTION IN YELLOWSTONE NATIONAL PARK -
LAKE ECONOMY, 1973.

Month	Sample	Food Item	Use	Elevation	Frequency	Percent	Percent	Importance	Importance
					Occurrence	Composition	of Diet		Value
					Percent	Per Item	Volume	Value	Percent
June	8	Graminae	Stems/Leaves/Heads	7800	87.5	76.4	66.9	58.5	89.90
		<i>Equisetum arvense</i>	Stems	7800	25.0	77.5	19.4	4.9	7.50
		<i>Heracleum lanatum</i>	Stems/Leaves	7800	12.5	100.0	12.5	1.6	2.40
		Cervidae	<i>Cervus canadensis</i>	7800	12.5	10.0	1.3	1.6	.24
		Avg.				7800			100.1
July	14	<i>Salmo alarki</i>	Entire	7800	50.0	67.9	33.9	17.00	45.0
		Graminae	Stems/Leaves/Heads	7800	50.0	54.3	27.1	13.60	36.0
		<i>Cirsium foliosum</i>	Stems/Heads	7800	21.4	63.3	13.6	2.90	7.7
		<i>Heracleum lanatum</i>	Stems/Leaves/Heads	7800	21.4	40.0	8.6	1.80	4.9
		<i>Equisetum arvense</i>	Stems	7800	14.3	75.0	10.7	1.50	4.1
		Cervidae	<i>Cervus canadensis</i>	7800	14.3	42.5	6.1	.87	2.3
Avg.				7800			100.0	37.67	100.0
Total									
Sample	22								

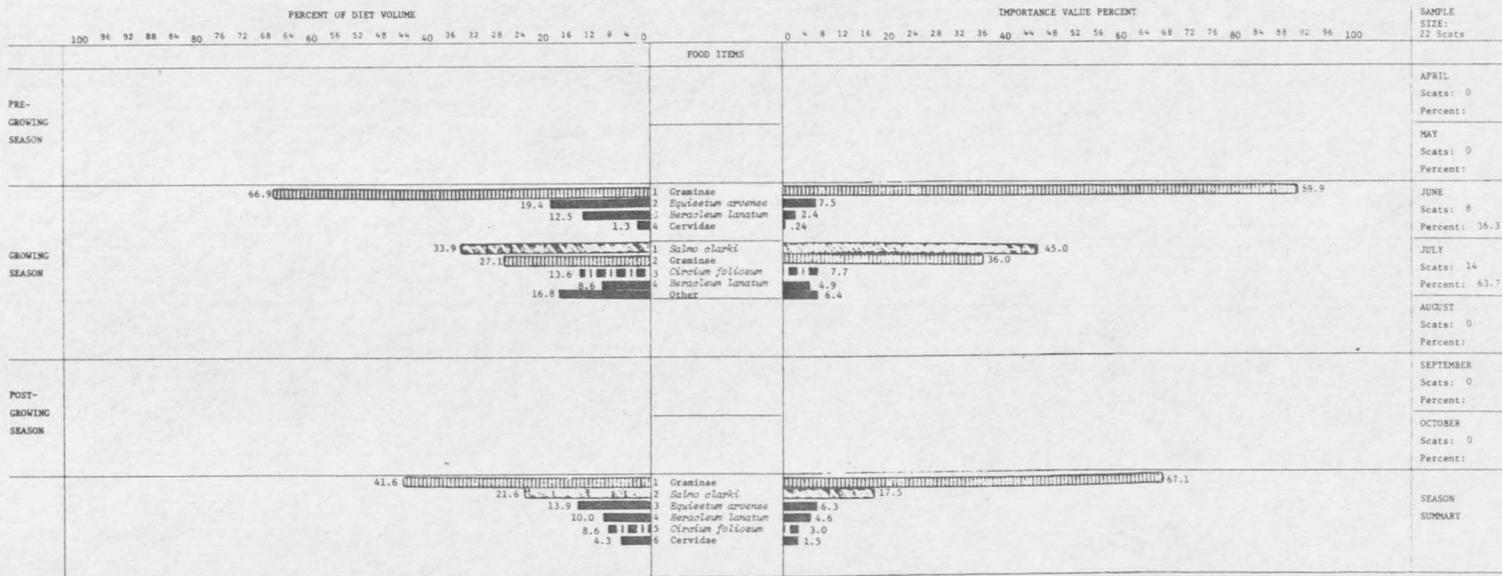


Figure 15. Grizzly bear seasonal food consumption in Yellowstone National Park - lake economy, 1973.

relatively high importance value percents were horsetail (*Equisetum arvense*) in June and elk thistle in July. For the year, grass was the most important food; percent composition per item of grass, cutthroat trout and horsetail indicate high levels of selection for these items (Table 15).

Table 16 and Figure 16 show food item consumption in 1974. They indicate that nearly 92 percent of the year's sample is listed for July. Cutthroat trout was the most important food with an importance value percent of 43.5. Grasses and sedges, elk thistle and horsetail ranked respectively below trout in the diet. In the annual summary (Table 17), data listed under Percent Composition Per Item show that while trout was the most highly selected food of the top ranking items, all foods were taken in combination with others.

Table 18 and Figure 17 compare the 1973 and 1974 annual lake economy summaries. The food items contributing to the diet were similar each year, but the rank orders and importance value percents are very different. The probable reason for the disparities is sampling differences between 1973 and 1974, which are apparent in Table 1.

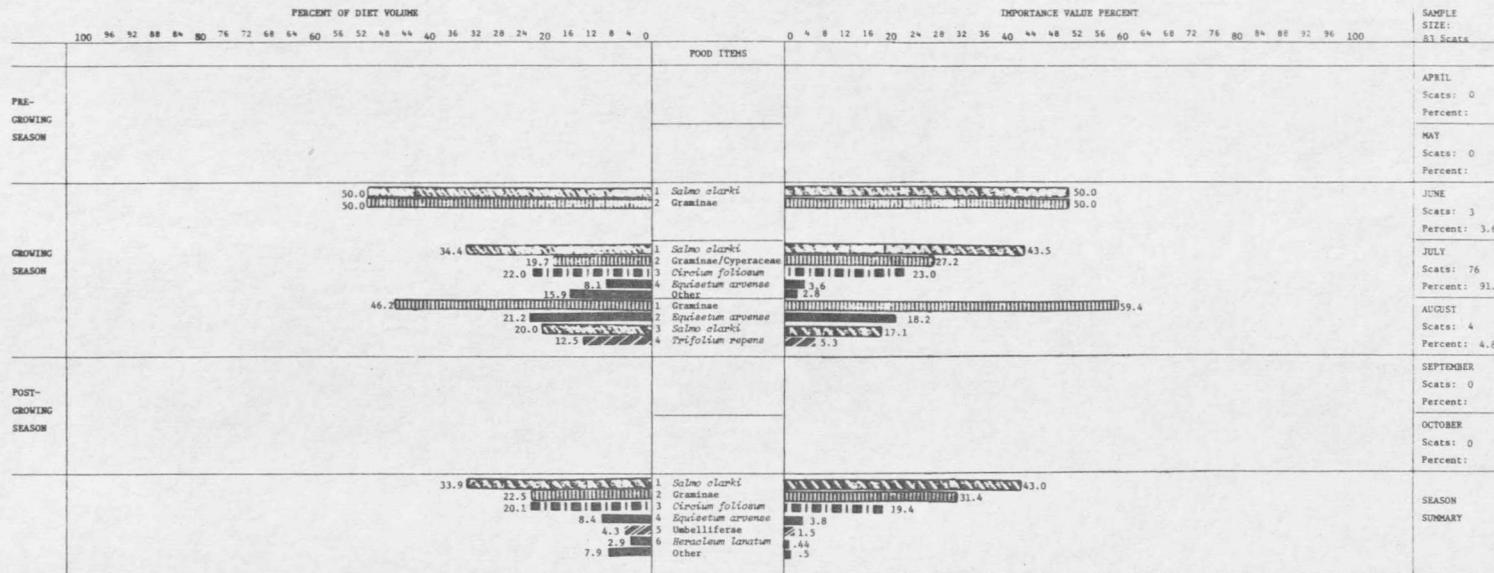
The two-year summaries (Table 19, Figure 17) indicate that grass and cutthroat trout were nearly equal in importance. The percent composition per item of trout indicates that this was the most highly selected of the most important food items.

TABLE 15. YELLOWSTONE NATIONAL PARK LAKE ECONOMY GRIZZLY BEAR FOOD CONSUMPTION
SUMMARY, 1973.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
Graminae	Stems/Leaves/Heads	7800	63.6	65.4	41.6	26.50	67.1
<i>Salmo clarki</i>	Entire	7800	31.8	67.9	21.6	6.90	17.5
<i>Equisetum arvense</i>	Stems	7800	18.2	76.3	13.9	2.50	6.3
<i>Heracleum lanatum</i>	Stems	7800	18.2	55.0	10.0	1.80	4.6
<i>Cirsium foliosum</i>	Stems/Heads	7800	13.6	63.3	8.6	1.20	3.0
Cervidae	<i>Cervus canadensis</i>	7800	13.6	31.7	4.3	.58	1.5
	Avg.	7800			100.0	39.48	100.0

TABLE 16. GRIZZLY BEAR SEASONAL FOOD CONSUMPTION IN YELLOWSTONE NATIONAL PARK -
LAKE ECONOMY, 1974.

Month	Sample	Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
June	3	<i>Salmo clarki</i>	Entire	7800	66.6	75.0	50.0	33.3	50.0
		Graminae	Stems/Leaves	7800	66.6	75.0	50.0	33.3	50.0
				Avg. 7800			100.0	66.6	100.0
July	76	<i>Salmo clarki</i>	Entire	7797	60.5	56.8	34.40	20.800	43.500
		Graminae/Cyperaceae	Graminae 90% Stems						
			<i>Carex</i> 10% Leaves	7810	66.0	29.9	19.70	13.000	27.200
		<i>Cirsium foliosum</i>	Stems/Heads	7821	50.0	44.0	22.00	11.000	23.000
		<i>Equisetum arvense</i>	Stems	7800	21.0	38.4	8.10	1.700	3.600
		Umbelliferae	<i>Perideridia gairdneri</i> - Roots	7807	18.4	25.3	4.70	.860	1.800
		<i>Heraclium lanatum</i>	Stems/Leaves	7767	8.0	40.0	3.20	.260	.540
		<i>Vaccinium scoparium</i>	Berries/Leaves	7800	2.6	100.0	2.60	.070	.140
		<i>Trifolium repens</i>	Stems/Leaves/Heads	7800	2.6	87.5	2.30	.060	.120
		Rodentia	<i>Thomomys talpoides</i>	7800	2.6	35.0	.92	.020	.050
		Formicidae	Mature/Larvae	7800	6.6	4.4	.29	.020	.040
		<i>Fragaria virginiana</i>	Fruits	7750	2.6	12.5	.33	.008	.020
		<i>Ruppia pectinata</i>	Stems/Leaves	7700	2.6	12.5	.33	.008	.020
		<i>Agoseris</i> sp.	Stems/Leaves/Heads	7800	1.3	35.0	.46	.006	.010
		Cervidae	<i>Cervus canadensis</i>	7800	1.3	25.0	.33	.004	.008
		<i>Anacharis</i> sp.	Stems/Leaves	7800	1.3	20.0	.36	.003	.006
		<i>Polygonum bistortoides</i>	Entire	7800	1.3	10.0	.13	.002	.004
		Avg. 7804				100.05	47.821	100.068	
August	4	Graminae	Stems/Leaves/Heads	7800	75.0	61.6	46.2	34.7	59.4
		<i>Equisetum arvense</i>	Stems	7800	50.0	42.5	21.2	10.6	18.2
		<i>Salmo clarki</i>	Entire	7800	50.0	40.0	20.0	10.0	17.1
		<i>Trifolium repens</i>	Stems/Leaves/Heads	7800	25.0	50.0	12.5	3.1	5.3
Total Sample	83			Avg. 7800			99.9	58.4	100.0



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Figure 16. Grizzly bear seasonal food consumption in Yellowstone National Park - lake economy, 1974.

TABLE 17. YELLOWSTONE NATIONAL PARK LAKE ECONOMY GRIZZLY BEAR FOOD CONSUMPTION SUMMARY, 1974.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
<i>Salmo clarki</i>	Entire	7797	60.2	56.4	33.90	20.400	43.000
Graminae	Stems/Leaves/Heads	7810	66.3	34.0	22.50	14.900	31.400
<i>Cirsium foliosum</i>	Stems/Heads	7821	45.8	44.0	20.10	9.200	18.400
<i>Equisetum arvense</i>	Stems	7800	21.7	38.9	8.40	1.800	3.800
Umbelliferae	<i>Perideridia gairdneri</i> - Roots	7807	16.9	25.3	4.30	.730	1.500
<i>Heraclium lanatum</i>	Stems	7767	7.2	40.0	2.90	.210	.440
<i>Trifolium repens</i>	Stems/Leaves/Heads	7800	3.6	75.0	2.70	.100	.210
<i>Vaccinium scoparium</i>	Berries/Leaves	7800	2.4	100.0	2.40	.060	.150
Rodentia	<i>Thomomys talpoides</i>	7800	2.4	35.0	.84	.020	.040
Formicidae	Mature/Larvae	7800	6.0	4.4	.27	.020	.040
<i>Fragaria virginiana</i>	Fruits	7750	2.4	12.5	.30	.007	.020
<i>Ruppia pectinata</i>	Entire	7700	2.4	12.5	.30	.007	.020
<i>Agoseris</i> sp.	Stems/Leaves	7800	1.2	35.0	.42	.005	.010
Cervidae	<i>Cervus canadensis</i>	7800	1.2	25.0	.30	.004	.008
<i>Anacharis</i> sp.	Stems/Leaves	7800	1.2	20.0	.24	.003	.006
<i>Polygonum bistortoides</i>	Entire	7800	1.2	10.0	.12	.001	.002
		Avg. 7804			99.99	47.467	100.026

TABLE 18. YELLOWSTONE NATIONAL PARK LAKE ECONOMY GRIZZLY BEAR KEY FOOD ITEM CONSUMPTION COMPARISON, 1973-1974.

Food Item	1973 Scat Sample - 22			Food Item	1974 Scat Sample - 83		
	Importance Value Percent	Percent Total Importance Value	Average Ele- vation		Importance Value Percent	Percent Total Importance Value	Average Ele- vation
Graminae	67.1			<i>Salmo clarki</i>	43.0		
<i>Salmo clarki</i>	17.5			Graminae	31.4		
<i>Equisetum arvense</i>	6.3			<i>Circium foliosum</i>	19.4		
<i>Heracleum lanatum</i>	4.6			<i>Equisetum arvense</i>	3.8		
<i>Circium foliosum</i>	3.0			Umbelliferae (roots)	1.5		
		98.5	7800			99.1	7804

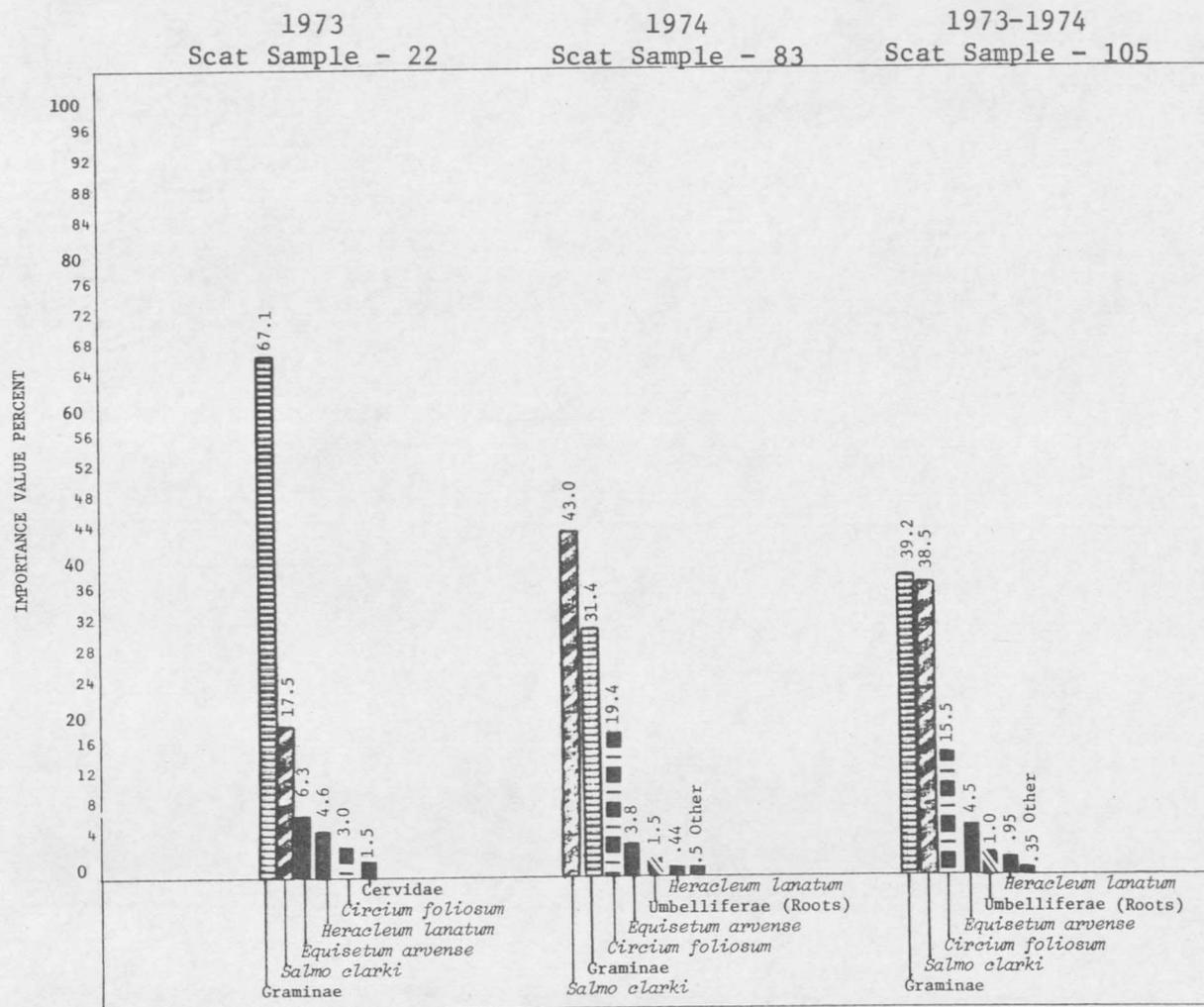


Figure 17. Yellowstone National Park lake economy grizzly bear key food item consumption comparison and summary, 1973-1974.

TABLE 19. YELLOWSTONE NATIONAL PARK LAKE ECONOMY GRIZZLY BEAR FOOD CONSUMPTION
SUMMARY, 1973-1974.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
Graminae	Stems/Leaves/Heads	7808	65.7	40.4	26.50	17.4000	39.200
<i>Salmo clarki</i>	Entire	7797	54.3	57.8	31.40	17.1000	38.500
<i>Cirsium foliosum</i>	Stems/Heads	7819	39.0	45.4	17.70	6.9000	15.500
<i>Equisetum arvense</i>	Stems	7800	21.0	45.7	9.60	2.0000	4.500
Umbelliferae	<i>Perideridia gairdneri</i> - Roots	7807	13.3	25.3	3.40	.4500	1.000
<i>Heracleum lanatum</i>	Stems/Leaves	7780	9.5	46.0	4.40	.4200	.950
<i>Trifolium repens</i>	Stems/Leaves/Heads	7800	2.8	75.0	2.10	.0600	.140
Cervidae	<i>Cervus canadensis</i>	7800	3.8	30.0	1.10	.0400	.090
<i>Vaccinium scoparium</i>	Berries/Leaves	7800	1.9	100.0	1.90	.0400	.090
Rodentia	<i>Thomomys talpoides</i>	7800	1.9	35.0	.66	.0100	.020
Formicidae	Mature/Larvae	7800	4.7	4.4	.21	.0100	.020
<i>Fragaria virginiana</i>	Fruits	7750	1.9	12.5	.24	.0040	.009
<i>Ruppia pectinata</i>	Entire	7700	1.9	12.5	.24	.0040	.009
<i>Agoseris</i> sp.	Stems/Leaves	7800	.95	35.0	.33	.0030	.007
<i>Anacharis</i> sp.	Stems/Leaves	7800	.95	20.0	.19	.0020	.005
<i>Polygonum bistortoides</i>	Entire	7800	.95	10.0	.09	.0009	.002
	Avg.	7803			100.06	44.4439	100.042

Field observations indicated that the feeding cycle was apparently directly related to the presence of spawning cutthroat trout in tributaries. This presence extended generally from late June to early August. Variation existed among individual tributaries in the actual time of occurrence of spawning trout (Knight, 1975).

Feeding activity in the economy is illustrated by observations made along a tributary at the tip of Flat Mountain Arm during the last half of July 1974. Estimated flow in the stream was $.13/m^3s$ and estimated peak fish density was six fish per linear meter within 0.8 km. of the mouth. Cutthroat trout caught personally in this segment averaged 38 cm. in length and 0.6 kg in weight. Eleven different grizzlies were sighted in the vicinity between July 16 and July 18, 1974 (Knight, 1975).

Bears moved in the stream and along the banks looking for vulnerable fish. Fish were often trapped against the bank and subsequently caught and eaten. Figure 14 shows this activity and the worn appearance of the stream bank. Cubs-of-the-year appeared to fish with an efficiency equal to or greater than that of adult bears (Graham, 1975^A). Grass, horsetail and elk thistle were heavily grazed in the area.

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

Summaries

Table 20 and Figure 18 show comparisons among the two-year summaries of food items consumed in each of the economies. For the valley/plateau economy data, seven items contribute 98.47 percent of total importance value. Grasses and sedges are by far the most important item with an importance value percent of 82. Average elevation of scat location is 7647 feet (2331 m.). For the mountain economy data, four items contribute 98.7 percent of total importance value. Western springbeauty is the most important item with an importance value percent of 55.5. Average elevation of scat location is 8969 feet (2734 m.). For the lake economy data, six items contribute 99.65 percent of total importance value. Grass and cutthroat trout are the most important items with importance values of 39.2 and 38.5, respectively. Average elevation of scat location is 7803 feet (2378 m.).

Of the 13 food items listed in Table 20, only three are listed under more than one economy. Grass and sedge occurs in the data of all three, elk thistle occurs in the valley/plateau and lake economy data and Umbelliferae roots appear in the mountain and lake economy data.

The data indicate substantial differences in diet compositions among economies. The valley/plateau economy apparently was grass-rodent oriented, the mountain economy springbeauty-grass-root oriented,

TABLE 20. GRIZZLY BEAR KEY FOOD ITEM CONSUMPTION COMPARISON AMONG YELLOWSTONE NATIONAL PARK ECONOMIES, 1973-1974:

Valley/Plateau Sample - 340				Mountain Sample - 170				Lake Sample - 105			
Food Item	Importance Value Percent	Percent		Food Item	Importance Value Percent	Percent		Food Item	Importance Value Percent	Percent	
		Total Importance Value	Average Ele- vation			Total Importance Value	Average Ele- vation			Total Importance Value	Average Ele- vation
Graminae/Cyperaceae	82.00			<i>Claytonia lanceolata</i>	55.5			Graminae	39.20		
<i>Trifolium repens</i>	5.30			Graminae/Cyperaceae	36.8			<i>Salmo clarki</i>	38.50		
<i>Cirsium foliosum</i>	3.30			Umbelliferae (Roots)	4.2			<i>Cirsium foliosum</i>	15.50		
Cervidae/Bovidae	2.80			<i>Pinus albicaulis</i>	2.2			<i>Equisetum arvense</i>	4.50		
Rodentia	2.30					98.7	8969	Umbelliferae (Roots)	1.00		
<i>Melica spectabilis</i> (Corms)	2.00							<i>Heracleum lanatum</i>	.95		
<i>Vaccinium scoparium</i>	.77									99.65	7803
		98.47	7647								

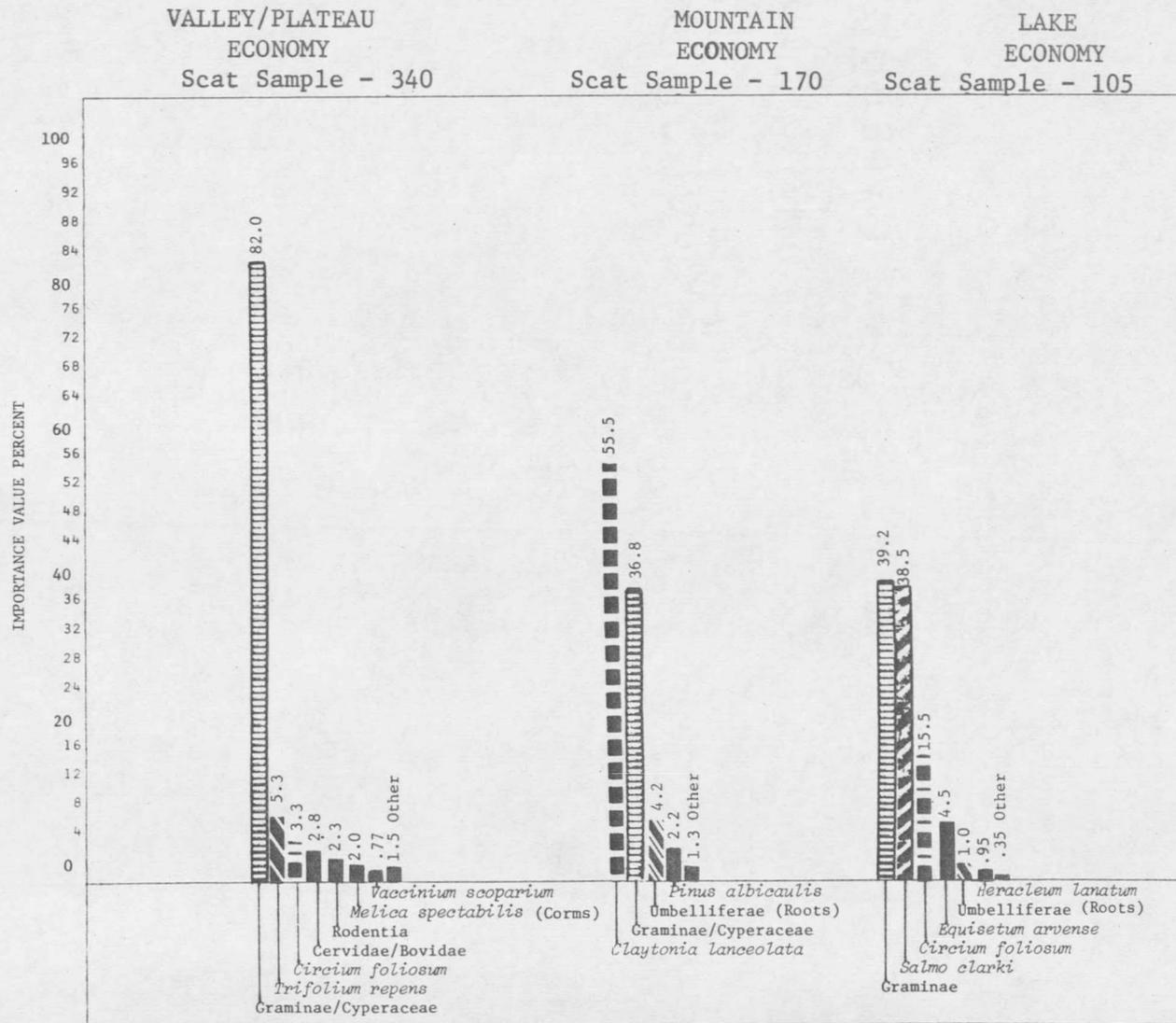


Figure 18. Grizzly bear key food item consumption comparison among Yellowstone National Park economies, 1973-1974.

and the lake economy grass-trout oriented.

Tables 21 and 22 present parkwide food consumption summaries for 1973 and 1974, respectively. Figure 19 shows a graphic comparison of these data. The diet each year was fairly constant. The most important items in 1973 were similar to those in 1974. Six items are common to the ranking of each year's eight top foods. Grasses and sedges, and western springbeauty rank first and second, respectively, in each year's data with comparable importance value percents. Cut-throat trout has a significantly higher importance value percent for 1974 because of increased sampling in the lake economy. High selection for springbeauty is shown both years.

Table 23 and Figure 19 show two-year parkwide summaries. Eight food items constituted 97.3 percent of the diet. Grasses and sedges were the ranking foods with an importance value percent of 78.5. Of the eight ranking food items, five were plant forms and represent 93.1 percent of total importance value. The remaining three items were fish and mammals and represent 4.3 percent of total importance value. Western springbeauty was the most highly selected of the major foods.

TABLE 21. YELLOWSTONE NATIONAL PARK PARKWIDE GRIZZLY BEAR FOOD CONSUMPTION SUMMARY, 1973.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
Graminae/Cyperaceae	Graminae 96% Stems Leaves						
	<i>Carex</i> sp. 4% Heads	7908	64.2	53.0	34.00	21.8000	73.600
<i>Claytonia lanceolata</i>	Entire	8830	15.6	69.8	11.00	1.7000	5.800
<i>Trifolium repens</i>	Stems/Leaves/Heads	7590	16.2	63.5	10.30	1.7000	5.600
<i>Cirsium foliosum</i>	Stems/Heads	7684	17.3	52.0	9.00	1.6000	5.400
Cervidae/Bovidae	<i>Cervus canadensis</i> 90% <i>Odocoileus hemionus</i> 5% <i>Bison bison</i> 5%	7522	11.7	54.1	6.40	.7500	2.500
Rodentia	<i>Thomomys talpoides</i> 50% <i>Microtus</i> 50%	7582	12.2	45.0	5.10	.6200	2.100
<i>Pinus albicaulis</i>	Nuts	8500	7.8	61.6	4.80	.3700	1.300
<i>Melica spectabilis</i>	Corms	7829	7.8	53.7	4.20	.3300	1.100
Umbelliferae	<i>Perideridia gairdneri</i> 54% - Roots <i>Lomatium cous</i> 46% - Roots	7646	7.3	41.2	3.00	.2200	.740
<i>Equisetum arvense</i>	Stems	8000	6.1	53.6	3.30	.2000	.670
<i>Salmo clarki</i>	Entire	7800	4.0	67.9	2.70	.1100	.370
Formicidae	Mature/Larvae	8133	13.4	3.9	.53	.0700	.230
<i>Heraclium lanatum</i>	Stems/Leaves	7908	3.3	49.2	1.70	.0600	.200
<i>Polygonum bistortoides</i>	Entire	7811	5.0	17.2	.90	.0500	.170
<i>Vaccinium scoparium</i>	Berries/Leaves	8080	2.8	35.6	1.00	.0300	.100
Garbage		7800	1.1	60.0	.67	.0070	.020
Vespidae	Mature/Leaves	7600	1.1	18.2	.20	.0020	.007
<i>Russula</i> sp.	Caps/Stems	8450	.56	30.0	.17	.0010	.003
<i>Ranunculus</i> sp.	Stems/Leaves/Flowers	8200	.56	10.0	.05	.0003	.001
					99.02	29.6203	99.911

TABLE 22. YELLOWSTONE NATIONAL PARK PARKWIDE GRIZZLY BEAR FOOD CONSUMPTION
SUMMARY, 1974.

Food Item	Use	Elevation	Frequency	Percent	Percent	Importance	Importance
			Occurrence	Composition	of Diet		Value
			Percent	Per Item	Volume		Percent
Graminae/Cyperaceae	Graminae 95%						
	Stems						
	Leaves						
	Heads	7988	64.7	56.2	36.40	23.6000	79.2000
<i>Carex</i> sp.	5%						
<i>Claytonia lanceolata</i>	Entire	9439	14.9	84.2	12.60	1.9000	6.3000
<i>Cirsium foliosum</i>	Stems/Heads	7902	15.8	48.2	7.60	1.2000	4.0000
<i>Salmo clarki</i>	Entire	7794	11.5	56.4	6.50	.7500	2.4000
Umbelliferae	<i>Perideridia gairdneri</i> 54% -						
	Roots						
	<i>Lomatium cous</i> 46% -	8439	12.4	41.7	5.20	.6400	2.2000
	Roots						
<i>Trifolium repens</i>	Stems/Leaves/Heads	7905	8.9	52.5	4.70	.4200	1.4000
Rodentia	<i>Thomomys talpoides</i> 71%						
	<i>Microtus</i> 26%						
	<i>Marmota flaviventris</i> 3%	7804	8.7	35.1	3.10	.2700	.9000
Cervidae/Bovidae	<i>Cervus canadensis</i> 90%						
	<i>Odocoileus hemionus</i> 7%						
	<i>Bison bison</i> 3%	7664	6.7	58.3	3.90	.2600	.8600
<i>Melica spectabilis</i>	Corns	7590	5.3	63.2	3.30	.1700	.5600
<i>Vaccinium scoparium</i>	Berries/Leaves	7857	4.8	70.0	3.40	.1600	.5400
<i>Equisetum arvense</i>	Stems	7860	5.5	47.2	2.50	.1400	.4600
<i>Pinus albicaulis</i>	Nuts	8361	3.9	50.0	2.00	.0800	.2600
Formicidae	Mature/Larvae	8280	6.9	14.2	1.00	.0700	.2400
<i>Heracleum lanatum</i>	Stems/Leaves	8162	3.0	46.1	1.40	.0400	.1300
<i>Russula</i> sp.	Caps/Stems	7935	3.0	25.4	.76	.0200	.0700
<i>Fragaria virginiana</i>	Fruits	8028	2.3	18.4	.42	.0100	.0300
<i>Polygonum bistortoides</i>	Entire	7806	2.5	21.4	.54	.0100	.3400
<i>Taraxicum</i> sp.	Stems/Leaves/Heads	7960	1.2	54.0	.62	.0070	.0200
<i>Smilacina</i> sp.	Rhizomes	8028	9.2	71.3	.65	.0060	.0200
Garbage		7778	.68	76.6	.53	.0040	.0100
<i>Agoseris</i> sp.	Stems/Leaves/Heads	7292	.68	76.6	.53	.0040	.0100
<i>Ribes setosum</i>	Berries	8600	.46	100.0	.46	.0020	.0070
Chlorophyceae	Entire	7400	.46	75.0	.34	.0020	.0070
Forb - U/I	Stems/Leaves	7050	.46	75.0	.34	.0020	.0070
<i>Mertensia ciliata</i>	Stems/Leaves	9325	.46	50.0	.23	.0010	.0030
<i>Ranunculus</i> sp.	Stems/Leaves/Flowers	7735	.46	40.0	.18	.0008	.0030
<i>Angelica</i> sp.	Stems/Leaves	7900	.46	27.5	.13	.0006	.0020
Vespidae	Mature/Larvae	7800	.46	30.0	.14	.0006	.0020
<i>Aster integrifolius</i>	Stems/Leaves	7800	.23	95.0	.21	.0005	.0020
<i>Pastinaca sativa</i>	Stems/Leaves	8900	.23	50.0	.11	.0003	.0010
<i>Ruppia pectinata</i>	Stems/Leaves	7700	.46	12.5	.06	.0003	.0010
<i>Anacharis</i> sp.	Entire	7800	.23	20.0	.05	.0001	.0003
					99.90	29.7712	99.9853

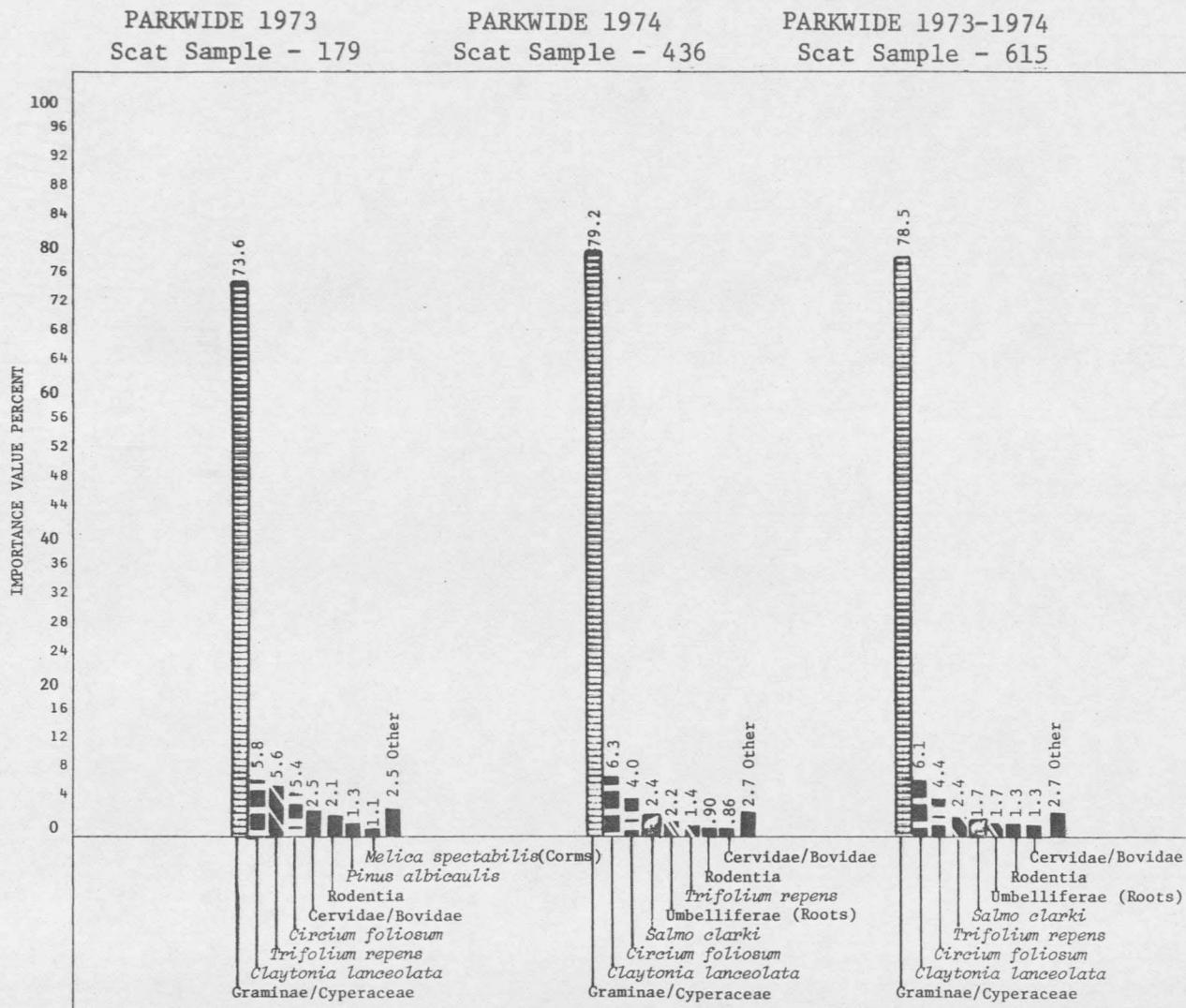


Figure 19. Yellowstone National Park, parkwide grizzly bear key food item consumption comparison and summary, 1973-1974.

TABLE 23. YELLOWSTONE NATIONAL PARK PARKWIDE GRIZZLY BEAR FOOD CONSUMPTION
SUMMARY, 1973-1974.

Food Item	Use	Elevation	Frequency Occurrence Percent	Percent Composition Per Item	Percent of Diet Volume	Importance Value	Importance Value Percent
Graminae/Cyperaceae	Graminae 95% Stems Leaves						
	<i>Carex</i> sp. 5% Heads	7965	64.5	55.3	35.70	23.00000	78.5000
<i>Claytonia lanceolata</i>	Entire	9256	15.1	79.9	12.10	1.80000	6.1000
<i>Cirsium foliosum</i>	Stems/Heads	7834	16.3	49.4	8.00	1.30000	4.4000
<i>Trifolium repens</i>	Stems/Leaves/Heads	7771	11.0	57.0	6.30	.69000	2.4000
<i>Salmo clarki</i>	Entire	7795	9.3	57.8	5.40	.50000	1.7000
Umbelliferae	<i>Perideridia gairdneri</i> 54% - Roots <i>Lomatium cous</i> 46% - Roots	8285	10.9	41.6	4.50	.49000	1.7000
Rodentia	<i>Thomomys talpoides</i> 63% <i>Microtus</i> 35% <i>Marmota flaviventris</i> 2%	7723	9.8	38.7	3.80	.37000	1.3000
Cervidae/Bovidae	<i>Cervus canadensis</i> 90% <i>Odocoileus hemionus</i> 6% <i>Bison bison</i> 4%	7604	8.1	56.5	4.60	.37000	1.3000
<i>Melica spectabilis</i>	Corms	7680	6.0	59.6	3.60	.22000	.7500
<i>Equisetum arvense</i>	Stems	7905	5.5	49.3	2.70	.15000	.5100
<i>Pinus albicaulis</i>	Nuts	8424	5.0	55.2	2.80	.14000	.4800
<i>Vaccinium scoparium</i>	Berries/Leaves	7900	4.2	63.4	2.70	.11000	.3700
Formicidae	Mature/Larvae	8215	8.8	9.6	.84	.07000	.2400
<i>Heracleum lanatum</i>	Stems/Leaves	8082	3.1	47.1	1.50	.04000	.1400
<i>Polygonium bistortoides</i>	Entire	7808	3.3	19.5	.63	.02000	.0700
<i>Russula</i> sp.	Caps/Stems	7972	2.3	25.7	.59	.01000	.0300
<i>Fragaria virginiana</i>	Fruits	8028	1.6	18.4	.30	.00500	.0200
Garbage		7787	.81	70.0	.57	.00500	.0200
<i>Taraxicum</i> sp.	Stems/Leaves/Heads	7960	.81	54.0	.44	.00400	.0100
<i>Smilacina</i> sp.	Rhizomes	8028	.65	71.3	.47	.00300	.0100
<i>Agoseris</i> sp.	Stems/Leaves/Heads	7292	.49	76.6	.37	.00200	.0070
Vespidae	Mature/Larvae	7700	.65	24.1	.16	.00100	.0030
<i>Ribes setosum</i>	Berries	8600	.33	100.0	.33	.00100	.0030
Chlorophyceae	Entire	7400	.33	75.0	.24	.00080	.0030
Forb - U/I	Stems/Leaves	7050	.33	75.0	.24	.00080	.0030
<i>Ranunculus</i> sp.	Stems/Leaves/Flowers	7890	.49	30.0	.15	.00070	.0020
<i>Mertensia ciliata</i>	Stems/Leaves	9325	.33	50.0	.16	.00050	.0020
<i>Angelica</i> sp.	Stems/Leaves	7900	.33	27.5	.09	.00030	.0010
<i>Aster integrifolius</i>	Stems/Leaves	7800	.16	95.0	.15	.00020	.0007
<i>Pastinaca sativa</i>	Stems/Leaves	8900	.16	50.0	.08	.00010	.0003
<i>Ruppia pectinata</i>	Stems/Leaves	7700	.33	12.5	.04	.00010	.0003
<i>Anacharis</i> sp.	Entire	7800	.16	20.0	.03	.00005	.0002
					99.58	29.30455	100.0755

Qualitative: Food Item Quality and Digestibility,
Nutrient Intake and Nutritive Values, Plant
Protein/Succulence-Flowering Relationship

Food Quality and Apparent Digestibility

Tables 24-35 present grizzly bear food quality and digestibility as indicated by chemical analysis. Foods are presented in rank order of consumption as they appear in Table 23.

In Table 24, the results of analysis of five different pairings of grass, and grass and sedge and corresponding scat material are shown. Food quality of individual items averaged 19.5 percent protein, 3.3 percent ether extract, and 45.2 percent nitrogen-free extract. Calculated energy averaged 3.3 kcals/gram. Digestibility of individual items averaged 42.0 percent for protein, 11.6 percent for ether extract, unknown for nitrogen-free extract (8.4 percent if the values for nitrogen-free extract are accepted, see footnote, Table 24) and 15.8 percent per gram of gross energy (21.5 percent per gram of gross energy if nitrogen-free extract values are accepted). Protein digestibility compares favorably with the 54 ± 12.3 percent reported for ruminants on roughage feeds including various grasses, legumes and native western hay (Crampton and Harris, 1969).

All five grass, grass/sedge samples in Table 24 were succulent when collected. The first two were collected before flowering, the last three after flowering. Protein content of pre-flowering material

TABLE 24. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS.

Principal Nutrient	Whole Food Material		Corresponding Scat Material		
	Proximate Content	Calculated Gross Kcals	Apparent Digested Kcals	Concentration Factor	Apparent Digestibility Percent
Item: <i>Agropyron</i> sp. - 50%, <i>Poa</i> sp. - 20%, <i>Bromus</i> sp. - 10%, <i>Phleum alpinum</i> - 10%, <i>Carex</i> sp. - 10%					
Economy: Mountain					
Condition: Pre-flowering, 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)	Unknown
Total		332.0	63.8		
Per Gram		3.3	.64		19.4
Item: <i>Poa</i> sp. - 50%, <i>Agropyron</i> sp. - 30%, <i>Phleum alpinum</i> - 10%, <i>Carex</i> sp. - 10%					
Economy: Mountain					
Condition: Pre-flowering, 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	.69		20.9
Item: <i>Deschampsia atropurpurea</i> - 80%, <i>Carex</i> sp. - 20%					
Economy: Mountain					
Condition: Post-flowering, 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	.32(.56)		10.7(18.8)
Item: <i>Poa</i> sp. - 100%					
Economy: Valley/Plateau					
Condition: Post-flowering, 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		3.8	.36(1.1)		9.5(28.9)
Item: <i>Calamagrostis inexpectata</i> - 100%					
Economy: Valley/Plateau					
Condition: Post-flowering, 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	.61(.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	.52(.73)		15.8(21.5)

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

was higher than that of post-flowering material, while the opposite was true of nitrogen-free extract. Energy/gram generally remained constant. A direct relationship between protein content and apparent protein digestibility is suggested by the data. Highest protein digestibility is recorded for the higher protein content pre-flowering samples, while lowest protein digestibility is recorded for the lower protein content post-flowering samples. This is to be expected because protein levels are highest in the aerial parts of plants during early growth stages and plant cell contents at this time are most available for digestion before cell walls lignify (Crampton and Harris, 1969; Klein, 1965).

If nitrogen-free extract values are accepted, a direct relationship between nitrogen-free extract content and digestibility is also suggested. No digestibility is apparent for the lower nitrogen-free extract content pre-flowering samples, while highest digestibility is recorded for the higher nitrogen-free extract content post-flowering samples.

If nitrogen-free extract values are accepted, the percents for apparent digestibility per gram of the gross energy of the five items in Table 24 are similar in spite of the differences between pre- and post-flowering condition in the relative amounts of protein and nitrogen-free extract and in their respective digestibilities. This suggests a digestive flexibility in grizzlies which may have provided

a relatively constant energy intake regardless of changes in diet levels of protein and nitrogen-free extract.

Ruch and Patton (1973) noted that both rats and man show a reduced capacity to catabolize glucose when on a high protein diet. A similar reduced capacity may also have been the case with high protein content and high digestibility and low (or no) nitrogen-free extract content and low digestibility associated with pre-flowering samples in Table 24. Presumably when diet protein is reduced, glucose catabolism increases as suggested by the data for post-flowering material.

Table 25 shows food quality and apparent digestibility of western springbeauty. Food quality of individual items 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 non-starch. Calculated energy averaged 4.0 kcals/gram. Digestibility of individual items averaged 61.8 percent for protein, 93.0 percent for starch, unknown for non-starch nitrogen-free extract (7.5 percent if the values are accepted) and 30.5 percent per gram of gross energy (35.0 percent per gram of gross energy if non-starch nitrogen-free extract values are accepted).

Pre-flowering material in Table 25 had higher protein content and higher protein digestibility than that of post-flowering material, while the opposite was true of nitrogen-free extract. Values for

TABLE 25. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS.

Item: *Claytonia lanceolata*

Consumption Rank: 2

Importance Value Percent: 6.1

Principal Nutrient	Whole Food Material		Corresponding Scat Material		
	Proximate Content	Calculated Gross Kcals	Apparent Digested Kcals	Concentration Factor	Apparent Digestibility Percent
Item: <i>Claytonia lanceolata</i> - 100%					
Economy: Mountain					
Condition: Pre-flowering, Succulent, Entire					
Protein	30.0	168.0	112.0	0	67.0
Ether Extract	2.8	26.0	Unknown	2.0	Unknown
Nitrogen-free Extract					
Starch*	11.3	48.6	45.2	0	93.0
Non-Starch	36.9	<u>158.7</u>	Unknown	Unknown(1.005)	Unknown
Total		401.3	157.2		
Per Gram		4.0	1.6		40.0
Item: <i>Claytonia lanceolata</i> - 100%					
Economy: Mountain					
Condition: Pre-flowering, Succulent, Above Ground					
Protein	39.0	218.4	150.6	0	69.0
Ether Extract	3.6	33.5	Unknown	1.9	Unknown
Nitrogen-free Extract	38.1	<u>163.8</u>	Unknown	Unknown(1.1)	Unknown
Total		415.7	150.6		
Per Gram		4.2	1.5		35.7
Item: <i>Claytonia lanceolata</i> - 100%					
Economy: Mountain					
Condition: Flowering, Succulent, Above Ground					
Protein	20.7	115.9	57.1	0	49.3
Ether Extract	5.4	50.2	Unknown	1.2	Unknown
Nitrogen-free Extract	50.8	<u>218.4</u>	Unknown(49.4)**	0	Unknown(22.6)
Total		384.5	57.1(106.5)		
Per Gram		3.8	.6(1.1)		15.8(28.9)
Averaged Values					
Protein	29.9	167.4	106.6	0	61.8
Ether Extract	3.9	36.6	Unknown	1.7	Unknown
Nitrogen-free Extract					
Starch	3.8	16.2	15.1	0	93.0
Non-Starch	41.9	<u>180.3</u>	Unknown(16.4)	0	Unknown(7.5)
Total		400.5	121.6(138.0)		
Per Gram		4.0	1.2(1.4)		30.5(35.0)

*Starch values determined by direct, starch-specific analysis.

**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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

digestibility per gram of gross energy of the three samples are comparable. This suggests an additional example of digestive flexibility providing constant energy intake regardless of changes in diet nutrient levels.

Table 26 shows white clover food quality and digestibility. None of the nutrients studied which were present in the whole food concentrated in the scats. This suggests that these nutrients were all probably readily digestible. Calculated energy averaged 3.6 kcals/gram and apparent digestibility per gram of gross energy averaged 13.9 percent (21.9 percent if nitrogen-free extract values are accepted).

Table 27 presents cutthroat trout food quality and digestibility. Averaged values for protein and ether extract content and digestibility are substantially higher than those recorded for succulent herbs (Tables 24-26). Ether extract of fish appears to consist 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 probably is made up primarily of phospholipids from cell membranes serving primarily as structural elements (Lehninger, 1973). Storage fats are more digestible than the waxy structural elements.

Table 28 shows the food quality and digestibility of Umbelliferae roots, melica grass corms and western springbeauty corms. The roots of biscuitroot, yampa (*Perideridia gairdneri*) and the corms of melica

TABLE 26. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS.

Item: *Trifolium repens*

Consumption Rank: 4

Importance Value Percent: 2.4

Principal Nutrient	Whole Food Material		Corresponding Scat Material		
	Proximate Content	Calculated Gross Kcals	Apparent Digested Kcals	Concentration Factor	Apparent Digestibility Percent
Item: <i>Trifolium repens</i> - 100%					
Economy: Valley/Plateau					
Condition: Flowering, Succulent					
Protein	22.0	123.2	45.9	0	37.3
Ether Extract	3.0	27.9	11.2	0	40.1
Nitrogen-free Extract	47.5	<u>204.3</u>	Unknown(14.7)*	0	Unknown(7.2)
Total		355.4	57.1(71.8)		
Per Gram		3.6	.57(.72)		15.8(20.0)
Item: <i>Trifolium repens</i> - 100%					
Economy: Valley/Plateau					
Condition: Flowering, Succulent					
Protein	23.1	129.4	39.2	0	30.3
Ether Extract	2.8	26.0	3.7	0	14.2
Nitrogen-free Extract	47.2	<u>202.9</u>	Unknown(43.8)	0	Unknown(21.6)
Total		358.3	42.9(86.7)		
Per Gram		3.6	.43(.87)		11.9(24.4)
Averaged Values					
Protein	22.5	126.3	42.6	0	33.8
Ether Extract	2.9	26.9	7.5	0	27.1
Nitrogen-free Extract	47.4	<u>203.6</u>	Unknown(29.3)	0	Unknown(14.4)
Total		356.8	50.0(79.3)		
Per Gram		3.6	.50(.79)		13.9(21.9)

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 27. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS.

Item: *Salmo clarki*
Consumption Rank: 5
Importance Value Percent: 1.7

Principal Nutrient	Whole Food Material		Corresponding Scat Material		
	Proximate Content	Calculated Gross Kcals	Apparent Digested Kcals	Concentration Factor	Apparent Digestibility Percent
Item: <i>Salmo clarki</i> - 100%					
Economy: Lake					
Condition: Without Eggs					
Protein	78.6	440.2	352.3	0	80.0
Ether Extract	8.2	76.3	63.3	0	82.9
Nitrogen-free Extract	0				
Total		516.5	415.6		
Per Gram		5.2	4.2		80.8
Item: <i>Salmo clarki</i> - 100%					
Economy: Lake					
Condition: With Eggs					
Protein	69.7	390.3	233.5	0	59.8
Ether Extract	23.0	213.9	199.0	0	93.0
Nitrogen-free Extract	1.0	4.3	Unknown	6.3	Unknown
Total		608.5	432.5		
Per Gram		6.1	4.3		70.5
Item: <i>Salmo clarki</i> - Eggs					
Economy: Lake					
Condition: Eggs Ripe					
Protein	68.5	383.6	279.4	0	72.8
Ether Extract	14.6	135.8	108.9	0	80.2
Nitrogen-free Extract	12.0	51.6	Unknown(12.5)*	0	Unknown(24.2)
Total		571.0	388.3(400.8)		
Per Gram		5.7	3.9(4.0)		68.4(70.3)
Averaged Values					
Protein	72.3	404.7	288.4	0	70.8
Ether Extract	15.3	142.0	123.7	0	85.3
Nitrogen-free Extract	4.3	18.5	Unknown(4.2)	2.1	Unknown(8.1)
Total		565.2	412.1(416.3)		
Per Gram		5.7	4.1(4.2)		73.2(73.7)

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 28. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS.

Item: Umbelliferae (with other starch sources for comparison)
 Consumption Rank: 6
 Importance Value Percent: 1.7

Principal Nutrient	Whole Food Material		Corresponding Scat Material		
	Proximate Content	Calculated Gross Kcals	Apparent Digested Kcals	Concentration Factor	Apparent Digestibility Percent
Item: <i>Lomatium cou</i> (Umbelliferae) - Roots - 100%					
Economy: Mountain					
Condition: Flowering					
Protein	6.0	33.6	11.8	0	35.0
Ether Extract	1.4	13.0	5.6	0	43.0
Nitrogen-free Extract					
Starch*	34.3	147.5	143.6	0	97.4
Non-Starch	43.3	186.2	Unknown(77.0)**	0	Unknown(41.5)
Total		380.3	161.0(238.0)		
Per Gram		3.8	1.6(2.4)		42.1(63.1)
Item: <i>Perideridia gairdneri</i> (Umbelliferae) - Roots - 100%					
Economy: Mountain					
Condition: Flowering					
Protein	4.8	26.9	4.5	0	16.7
Ether Extract	.5	4.7	Unknown	2.0	Unknown
Nitrogen-free Extract					
Starch	40.1	172.4	99.3	0	57.6
Non-Starch	47.5	204.3	Unknown(21.1)	0	Unknown(10.3)
Total		408.3	103.8(124.9)		
Per Gram		4.1	1.0(1.2)		24.4(29.3)
Item: <i>Melica spectabilis</i> - Corms - 100%					
Economy: Valley/Plateau					
Condition: Flowering					
Protein	6.1	34.2	13.5	0	39.5
Ether Extract	.4	3.7	1.8	0	48.6
Nitrogen-free Extract					
Starch	10.4	44.7	30.1	0	67.3
Non-Starch	78.3	336.7	Unknown(30.1)	0	Unknown(8.9)
Total		419.3	45.4(75.5)		
Per Gram		4.2	.45(.76)		10.7(18.1)
Item: <i>Claytonia lanceolata</i> - Corms - 100%					
Economy: Mountain					
Condition: Pre-flowering, Succulent					
Protein	12.1	67.8	Unknown	Unknown	Unknown
Ether Extract	1.6	14.9	Unknown	Unknown	Unknown
Nitrogen-free Extract					
Starch	11.3	48.6	45.2	0	93.0
Non-Starch	55.4	238.2	Unknown	Unknown	Unknown
Total		369.5	Unknown		
Per Gram		3.7	Unknown		Unknown
Averaged Values					
Protein	7.3	40.6	9.9	0	30.4
Ether Extract	1.0	9.1	2.5	0	30.5
Nitrogen-free Extract					
Starch	24.0	103.3	79.6	0	78.8
Non-Starch	56.1	274.2	Unknown(42.7)	0	Unknown(20.2)
Total		394.4	103.4(146.1)		
Per Gram		3.9	1.0(1.5)		25.7(36.8)

*Starch values determined by direct, starch-specific analysis.

**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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

grass were collected at about the same stage of maturity. Starch content of the corms was much lower than that of the roots; digestibility of starch in corms was comparable with that in roots. The lower starch content of melica corms is reflected in the 10.7 percent digestibility per gram of gross energy. This compares with 42.1 percent for biscuitroot and 24.4 percent for yampa. Two other indicators identified melica corms as having lower food value than biscuitroot and yampa: 1) after having been ground in a Wiley Mill, melica corms retained a coarse, granulated appearance while both biscuitroot and yampa, after the same treatment, had the appearance of very fine flour; 2) melica corms in scats appeared nearly intact, while roots of biscuitroot and yampa in scats were greatly altered. The data show that western springbeauty corms are low (11.3 percent) in starch in pre-flowering condition. After flowering, springbeauty corms are full, fleshy and starch levels are probably much higher than 11.3 percent due to replenishment of carbohydrate stores depleted during growth initiation (Klein, 1965).

Food quality and digestibility of elk tissue and pine nuts are presented respectively in Tables 29 and 30. The high digestibility of elk protein and storage fat is apparent in Table 29. In Table 30, the high energy and digestibility of storage fats in pine nuts are apparent.

TABLE 29. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS.

Item: Cervidae/Bovidae

Consumption Rank: 8

Importance Value Percent: 1.3

Principal Nutrient	Whole Food Material		Corresponding Scat Material		
	Proximate Content	Calculated Gross Kcals	Apparent Digested Kcals	Concentration Factor	Apparent Digestibility Percent
Item: <i>Cervus canadensis</i> - 100%					
Economy: Valley/Plateau					
Condition: Lean Tissue					
Protein	88.20	493.90	414.4	0	83.9
Ether Extract	6.70	62.30	54.4	0	87.3
Nitrogen-free Extract	.11	.47	Unknown	161.8	Unknown
Total		556.70	468.8		
Per Gram		5.6	4.7		83.9
Item: <i>Cervus canadensis</i>					
Economy: Valley/Plateau					
Condition: Lean Tissue					
Protein	88.20	493.90	404.8	0	81.9
Ether Extract	6.70	62.30	39.0	0	62.6
Nitrogen-free Extract	.11	.47	Unknown	111.8	Unknown
Total		556.70	443.8		
Per Gram		5.6	4.4		78.6
Averaged Values					
Protein	88.20	493.90	409.6	0	82.9
Ether Extract	6.70	62.30	46.7	0	74.9
Nitrogen-free Extract	.11	.47	Unknown	136.8	Unknown
Total		556.70	456.3		
Per Gram		5.6	4.6		81.3

TABLE 30. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS.

Item: *Pinus albicaulis*

Consumption Rank: 11

Importance Value Percent: .48

Principal Nutrient	Whole Food Material		Corresponding Scat Material		
	Proximate Content	Calculated Gross Kcals	Apparent Digested Kcals	Concentration Factor	Apparent Digestibility Percent
Item: <i>Pinus albicaulis</i> - Nuts - 100%					
Economy: Mountain					
Condition: Mature					
Protein	11.9	66.6	29.0	0	42.0
Ether Extract	21.8	202.8	193.5	0	95.4
Nitrogen-free Extract	27.2	<u>116.9</u>	Unknown(14.1)*	0	Unknown(12.1)
Total		386.3	221.5(235.6)		
Per Gram		3.9	2.2(2.4)		56.4(61.5)
Item: <i>Pinus albicaulis</i> - Nuts - 100%					
Economy: Mountain					
Condition: Mature					
Protein	11.9	66.6	34.1	0	51.2
Ether Extract	21.8	202.8	126.5	0	62.4
Nitrogen-free Extract	27.2	<u>116.9</u>	Unknown(6.8)	0	Unknown(5.8)
Total		386.3	160.6(167.4)		
Per Gram		3.9	1.6(1.7)		41.0(43.5)
Averaged Values					
Protein	11.9	66.6	31.1	0	46.6
Ether Extract	21.8	202.8	160.0	0	78.9
Nitrogen-free Extract	27.2	<u>116.9</u>	Unknown(10.5)	0	Unknown(9.0)
Total		386.3	191.1(201.5)		
Per Gram		3.9	1.9(2.1)		48.7(52.5)

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

Table 31 presents the food quality and digestibility of horse-tail and mushroom. Mushroom, ranking 16th out of 32 food items consumed, was 23.3 percent protein and contained 3.9 kcals/gram of calculated energy. Protein was 66.5 percent digestible. Ether extract, primarily storage fat (Jackson, 1975) was 46.5 percent digestible.

The food quality of seven additional foods is shown in Tables 32-34. Food quality of ripe berries and fruits is shown in Table 33. Individual items averaged 8.9 percent protein, 6.2 percent ether extract and 66.0 percent nitrogen-free extract. Calculated energy averaged 3.9 kcals/gram. In Table 34 the average value for protein content of cowparsnip (*Heracleum lanatum*) is 5.7 percent. Klein (1965) reported protein values of 36.1 and 20.6 percent for the same species in southeast Alaska.

Table 35 provides a summary of grizzly bear food quality and digestibility. Items are ranked by their digestibility. Animal material has the highest digestibility and the highest calculated energy content. 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 also apparent.

TABLE 31. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS.

Principal Nutrient	Whole Food Material		Corresponding Scat Material		
	Proximate Content	Calculated Gross Kcals	Apparent Digested Kcals	Concentration Factor	Apparent Digestibility Percent
Item: <i>Equisetum arvense</i>					
Consumption Rank: 10					
Importance Value Percent: .51					
Item: <i>Equisetum arvense</i>					
Economy: Lake					
Condition: Sterile Shoots					
Protein	15.0	84.0	26.3	0	31.3
Ether Extract	3.7	34.4	10.2	0	29.6
Nitrogen-free Extract	40.6	<u>174.6</u>	<u>Unknown</u>	1.1	<u>Unknown</u>
Total		293.0	36.5		
Per Gram		2.9	.37		12.8
Item: <i>Russula</i> sp.					
Consumption Rank: 16					
Importance Value Percent: .03					
Item: <i>Russula</i> sp.					
Economy: Valley/Plateau					
Condition: Mature					
Protein	23.3	130.5	86.8	0	66.5
Ether Extract	2.8	26.0	12.1	0	46.5
Nitrogen-free Extract	53.7	<u>230.9</u>	<u>Unknown(31.4)*</u>	0	<u>Unknown(13.6)</u>
Total		387.4	98.9(130.3)		
Per Gram		3.9	.98(1.3)		25.0(33.0)

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 32. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS.

Principal Nutrient	Whole Food Material	
	Proximate Content	Calculated Gross Kcals
Item: <i>Cirsium foliosum</i> Consumption Rank: 3 Importance Value Percent: 4.4		
Species: <i>Cirsium foliosum</i> - 100% Economy: Valley/Plateau Condition: Pre-flowering, Succulent		
Protein	9.0	50.4
Ether Extract	1.8	16.7
Nitrogen-free Extract	52.3	224.9
Total Per Gram		292.0 2.9
Item: Rodentia Consumption Rank: 7 Importance Value Percent: 1.3		
Species: <i>Microtus</i> sp. - 100% Economy: Valley/Plateau Condition: Mature		
Protein	69.8	390.9
Ether Extract	8.7	80.9
Nitrogen-free Extract	3.7	15.9
Total Per Gram		487.7 4.9
Item: <i>Polygonum bistortoides</i> Consumption Rank: 15 Importance Value Percent: .07		
Species: <i>Polygonum bistortoides</i> , Roots - 100% Economy: Mountain Condition: Flowering, Succulent		
Protein	11.0	61.6
Ether Extract	1.2	11.2
Nitrogen-free Extract	71.4	307.0
Total Per Gram		379.8 3.8

TABLE 33. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS.
 Item: *Vaccinium scoparium* (with other sugar sources for comparison)
 Consumption Rank: 12
 Importance Value Percent: .37

Principal Nutrient	Whole Food Material	
	Proximate Content	Calculated Gross Kcals
Species: <i>Vaccinium scoparium</i> - 100%		
Economy: Valley/Plateau		
Condition: Ripe Berries		
Protein	9.7	54.3
Ether Extract	6.1	56.7
Nitrogen-free Extract	67.8	291.5
Total Per Gram		402.5 4.0
Species: <i>Ribes setosum</i> - 100%		
Economy: Mountain		
Condition: Ripe Berries		
Protein	7.2	40.3
Ether Extract	5.2	48.4
Nitrogen-free Extract	66.7	286.8
Total Per Gram		375.5 3.8
Species: <i>Fragaria virginiana</i> - 100%		
Economy: Valley/Plateau		
Condition: Ripe Fruits		
Protein	9.8	54.9
Ether Extract	7.5	69.8
Nitrogen-free Extract	63.6	273.5
Total Per Gram		398.2 4.0
Averaged Values		
Protein	8.9	49.8
Ether Extract	6.2	57.7
Nitrogen-free Extract	66.0	283.8
Total Per Gram		391.3 3.9

TABLE 34. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS.

Item: *Heracleum lanatum*
 Composition Rank: 14
 Importance Value Percent: .14

Principal Nutrient	Whole Food Material	
	Proximate Content	Calculated Gross Kcals
Species: <i>Heracleum lanatum</i> - 100%		
Economy: Valley/Plateau		
Condition: Pre-flowering, Succulent		
Protein	7.3	40.9
Ether Extract	2.2	20.5
Nitrogen-free Extract	44.5	<u>191.4</u>
Total Per Gram		252.8 2.5
Species: <i>Heracleum lanatum</i> - 100%		
Economy: Valley/Plateau		
Condition: Post-flowering, Succulent		
Protein	4.1	23.0
Ether Extract	1.5	14.0
Nitrogen-free Extract	43.5	<u>187.1</u>
Total Per Gram		224.1 2.2
Averaged Values		
Protein	5.7	31.9
Ether Extract	1.9	17.7
Nitrogen-free Extract	44.0	<u>189.7</u>
Total Per Gram		239.3 2.4

TABLE 35. SUMMARY: GRIZZLY BEAR FOOD ITEM QUALITY AND DIGESTIBILITY.

Food Item	Apparent Digested Kcals/Gram	Apparent Digestibility Percent	Calculated Kcals/Gram Whole Food	Consumptive Use Rank
Cervidae/Bovidae	4.6	81.3	5.6	8
<i>Salmo clarki</i>	4.1 (4.2)*	73.2 (73.7)	5.7	5
<i>Pinus albicaulis</i> (Nuts)	1.9 (2.1)	48.7 (52.5)	3.9	11
<i>Claytonia lanceolata</i>	1.2 (1.4)	30.5 (35.0)	4.0	2
Umbelliferae (Roots) plus corms of <i>Melica spectabilis</i> and <i>Claytonia lanceolata</i>	1.0 (1.5)	25.7 (36.8)	3.9	6
<i>Russula</i> sp.	.98 (1.3)	25.0 (33.0)	3.9	16
Graminae/Cyperaceae	.52 (.73)	15.8 (21.5)	3.3	1
<i>Trifolium repens</i>	.50 (.79)	13.9 (21.9)	3.6	4
<i>Equisetum arvense</i>	.37	12.8	2.9	10

*Results in parentheses include nitrogen-free extract values.

Nutrient Intake and Nutritive Values

The five principal nutrient materials contributing to total grizzly energy intake are listed in Table 36 with their sources and estimated digestibilities. These data were derived from data in Tables 24-34. Protein from succulent herbs is estimated to be 42.8 percent digestible, protein and fat from animal material is estimated to be 78.1 percent digestible, fat and protein from whitebark pine nuts is estimated to be 73.6 percent digestible, starch from herbs is estimated to be 78.8 percent digestible, and the digestibility of sugar from berries and fruits of shrubs and herbs is undetermined.

Table 37 and Figures 20 and 21 present 1974 seasonal grizzly nutrient intake and nutritive values for the valley/plateau economy. Figure 20 shows nutrient importance values which equate to quantitative nutrient intake, Figure 21 shows nutritive value percents which are nutrient importance values modified by their respective digestibilities. Nutritive value percents represent estimates of each nutrient's contribution towards the grizzly's energy intake. All data show that animal protein and fat were the principal nutrients during much of the pre-growing season. They were replaced as the primary nutrients by protein from succulent herbs towards the end of the pre-growing season. Protein from succulent herbs remained the most important nutrient throughout the rest of the year, but declined somewhat

TABLE 36. PRINCIPAL GRIZZLY BEAR FOOD NUTRIENTS AND DIGESTIBILITIES.

Principal Nutrient	Source*	Apparent Digestibility Percent**
Protein	Succulent Herbs	42.8
Protein, Fat	Animal	78.1
Fat, Protein	<i>Pinus albicaulis</i>	73.6
Starch	Herbs	78.8
Sugar	Shrubs; Herbs	Undetermined

*Succulent Herbs: Graminae, Cyperaceae, *Claytonia lanceolata*, *Cirsium foliosum*, *Trifolium repens*, *Equisetum arvense*, etc.

Animal: Cervidae, Bovidae, *Salmo clarki*, Rodentia, Formicidae, Vespidae.

Herbs - starch: *Perideridia gairdneri*, *Lomatium cous*, *Claytonia lanceolata*, *Polygonum bistortoides*, *Melica spectabilis*, *Smilacina* sp.

Shrubs and Herbs - sugar: *Vaccinium scoparium*, *Ribes setosum*, *Fragaria virginiana*.

**Values are weighted averages.

TABLE 37. 1974 SEASONAL GRIZZLY BEAR NUTRIENT INTAKE AND NUTRITIVE VALUES - VALLEY/PLATEAU ECONOMY.

Month	Scat Sample	Principal Nutrients	Source	Frequency of Occurrence Percent	Percent of Diet Volume	Importance Value	Importance Value Percent	Apparent Digestibility Percent	Nutritive Value Index Percent	
April	7	Protein	Succulent Herbs	28.5	17.0	4.8	6.3	42.8	2.7	3.6
		Protein, Fat	Animal	85.7	82.8	70.9	93.6	78.1	73.1	96.4
Total					99.8	75.7	99.9		75.8	100.0
May	31	Protein	Succulent Herbs	67.7	49.9	33.7	57.4	42.8	24.6	42.6
		Protein, Fat	Animal	61.2	32.9	20.1	34.3	78.1	26.7	46.2
		Starch	Herbs	29.0	16.9	4.9	8.3	78.8	6.5	11.3
Total					99.7	58.7	99.9		57.8	100.1
June	23	Protein	Succulent Herbs	95.6	75.9	72.50	93.50	42.8	40.0	88.7
		Protein, Fat	Animal	26.0	17.4	4.50	5.80	78.1	4.5	10.0
		Starch	Herbs	8.7	6.5	.56	.72	78.8	.6	1.3
Total					99.8	77.56	100.02		45.1	100.0
July	35	Protein	Succulent Herbs	97.1	86.1	69.5	93.90	42.8	40.20	89.4
		Protein, Fat	Animal	48.6	7.8	3.8	5.10	78.1	4.00	8.9
		Starch	Herbs	11.4	6.1	.7	.95	78.8	.75	1.7
Total					100.0	74.0	99.95		44.95	100.0
August	42	Protein	Succulent Herbs	88.1	82.30	72.500	94.900	42.8	40.600	96.90
		Protein, Fat	Animal	14.3	1.30	.180	.230	78.1	.200	.50
		Fat, Protein	<i>Pinus albicaulis</i>	2.4	.24	.006	.007	73.6	.005	.01
		Starch	Herbs	28.6	3.90	1.100	1.400	78.8	1.100	2.60
		Sugar	Shrubs, Herbs	21.4	12.10	2.600	3.400	Unknown	----	----
Total					99.84	76.386	99.937		41.905	100.01
September	50	Protein	Succulent Herbs	80.0	59.3	47.40	86.90	42.8	37.20	89.50
		Protein, Fat	Animal	6.0	1.7	.10	.18	78.1	.14	.34
		Fat, Protein	<i>Pinus albicaulis</i>	8.0	5.7	.46	.84	73.6	.62	1.50
		Starch	Herbs	20.0	12.3	2.50	4.60	78.8	3.62	8.71
		Sugar	Shrubs, Herbs	26.0	15.7	4.10	7.50	Unknown	----	----
Total					94.7	54.56	100.02		41.58	100.05
October	32	Protein	Succulent Herbs	78.1	55.8	43.60	72.60	42.8	31.1	59.1
		Protein, Fat	Animal	43.7	20.5	8.90	14.80	78.1	11.6	22.1
		Starch	Herbs	34.4	21.8	7.50	12.50	78.8	9.9	18.8
		Sugar	Shrubs, Herbs	3.1	1.6	.05	.08	Unknown	----	----
Total					99.7	60.05	99.98		52.6	100.0
Annual Summary										
	220	Protein	Succulent Herbs	80.0	67.3	53.80	88.10	42.8	37.70	81.7
		Protein, Fat	Animal	32.3	13.4	4.30	7.00	78.1	5.50	11.9
		Fat, Protein	<i>Pinus albicaulis</i>	2.2	1.3	.03	.05	73.6	.04	.1
		Starch	Herbs	21.8	10.7	2.30	3.70	78.8	2.90	6.3
		Sugar	Shrubs, Herbs	10.5	6.1	.64	1.10	Unknown	----	----
Total					98.8	61.07	99.95		46.14	100.0

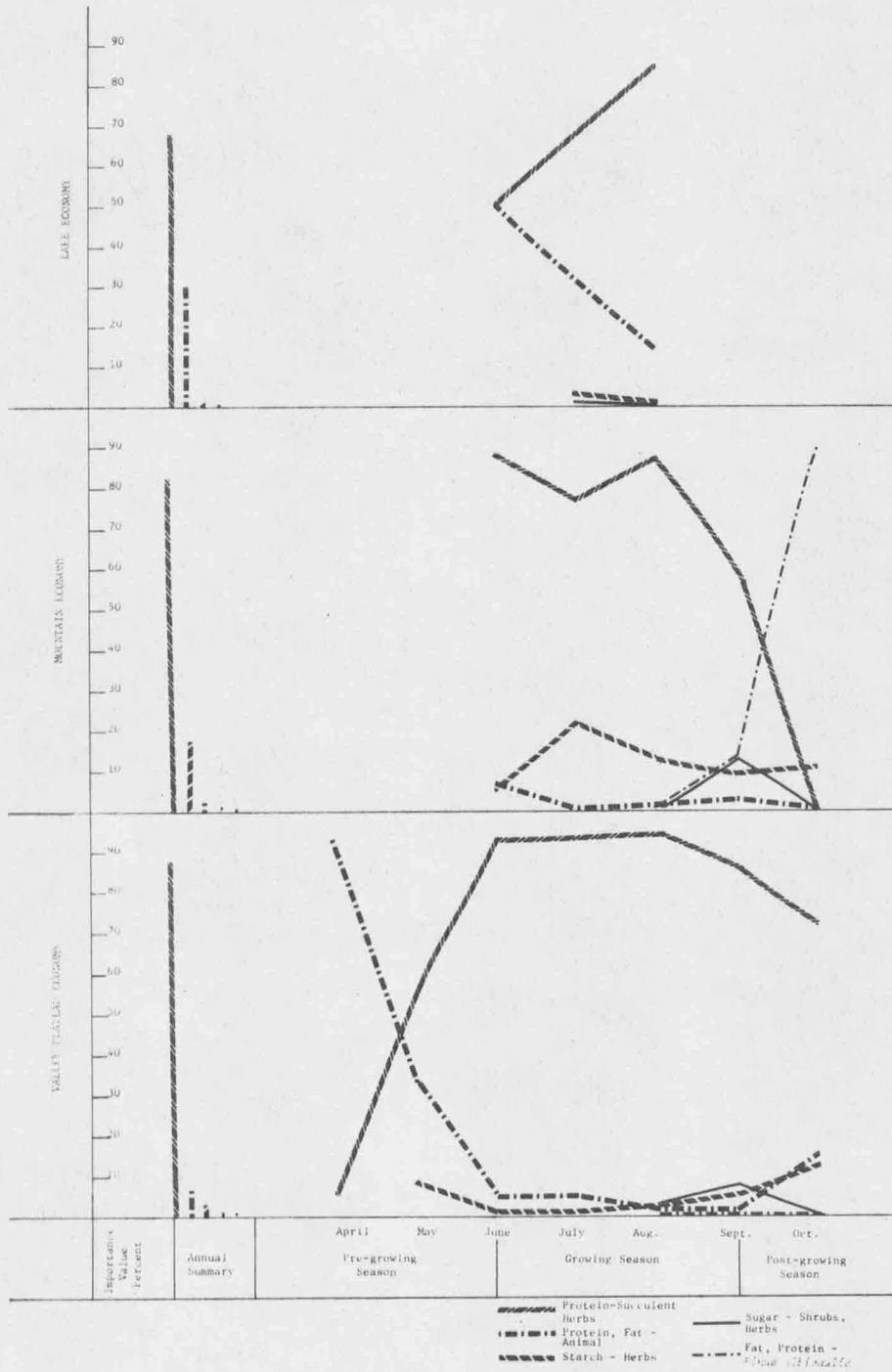


Figure 20. Seasonal nutrient importance value comparison among Yellowstone National Park grizzly bear food economies, 1974.

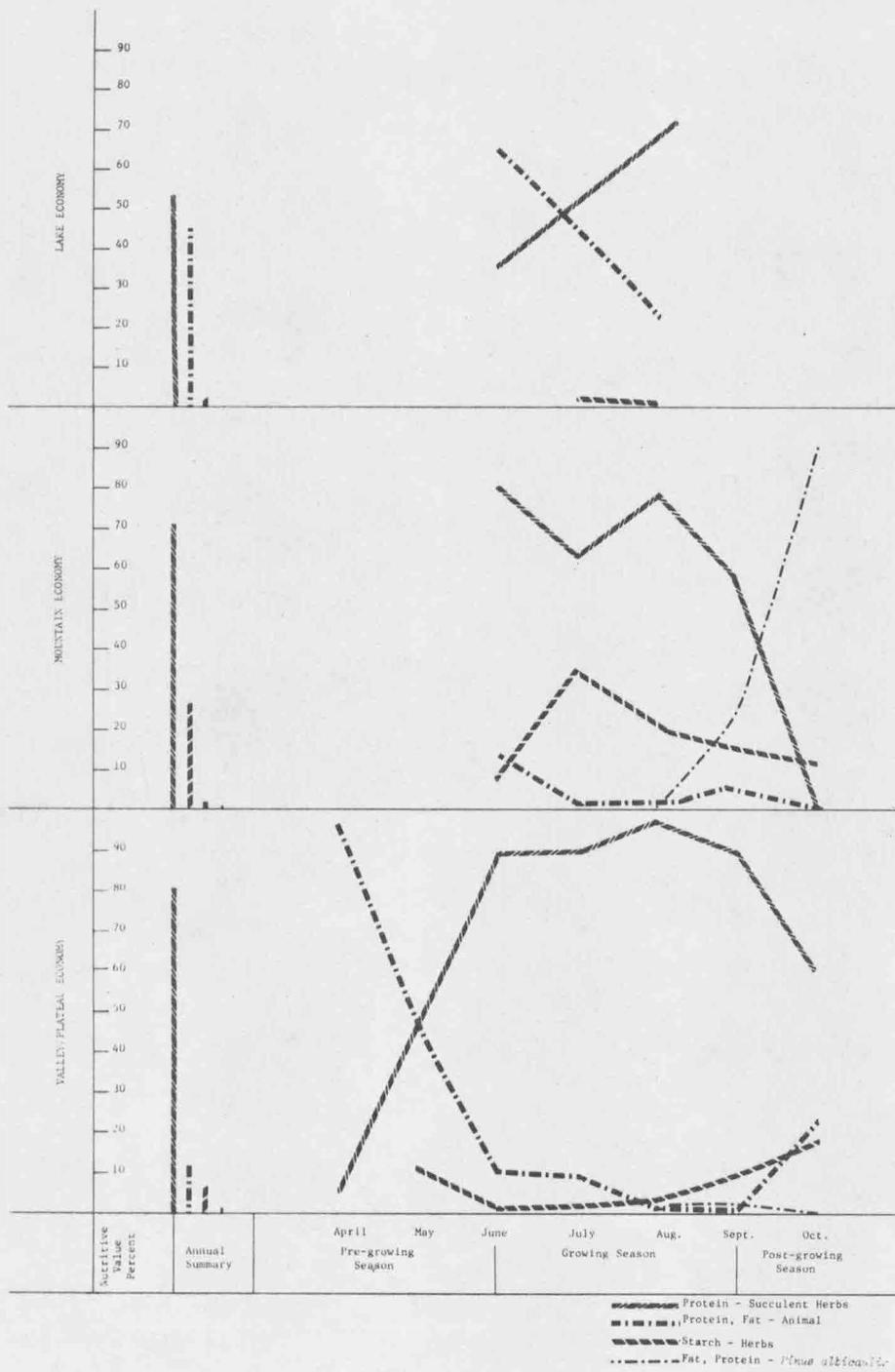


Figure 21. Seasonal nutritive value comparison among Yellowstone National Park grizzly bear food economies, 1974.

during the post-growing season. Starch had some importance during the pre- and post-growing seasons, and sugars and protein and fat from whitebark pine nuts and animals (elk) were important in the post-growing season. The nutritive value percent annual summaries show that protein from succulent herbs contributed 81.7 percent of the grizzly's energy intake, animal protein and fat contributed 11.9 percent and starch contributed 6.3 percent. Sugar was not calculated, but owing to its low importance value percent of 1.1, its nutritive value percent would not have changed the annual summary data significantly.

Table 38 and Figures 20 and 21 present 1974 seasonal grizzly nutrient intake and nutritive values for the mountain economy. No data are available for the pre-growing season. All data indicate that during the growing season, protein from succulent herbs was the most important nutrient and starch was the second most important nutrient. Western springbeauty was the primary source of starch. Corn remains were estimated to make up 20 percent of scats containing primarily springbeauty residues. During the post-growing season, the importance of protein from succulent herbs declined while the importance of fat and protein from whitebark pine nuts increased. The importance of starch remained relatively constant. The nutritive value percent annual summaries show that protein from succulent herbs contributed 71.7 percent of the grizzly's energy intake, starch contributed 26.3

TABLE 38. 1974 SEASONAL GRIZZLY BEAR NUTRIENT INTAKE AND NUTRITIVE VALUES -- MOUNTAIN ECONOMY.

Month	Scat Sample	Principal Nutrient	Source	Frequency of Occurrence Percent	Percent of Diet Volume	Importance Value	Importance Value Percent	Apparent Digestibility Percent	Nutritive Value	
									Index	Percent
June	4	Protein	Succulent Herbs	100.0	72.4	72.4	88.1	42.8	37.7	80.2
		Protein, Fat	Animal	50.0	12.0	6.0	7.3	78.1	5.7	12.1
		Starch	Herbs	25.0	15.0	3.8	4.6	78.8	3.6	7.7
		Total				99.4	82.2	100.0		47.0
July	52	Protein	Succulent Herbs	96.2	74.0	71.20	77.60	42.8	33.2	63.4
		Protein, Fat	Animal	13.5	2.7	.36	.39	78.1	.3	.6
		Starch	Herbs	86.5	23.3	20.20	22.00	78.8	17.3	34.1
		Total				100.0	91.76	99.99		50.8
August	60	Protein	Succulent Herbs	91.6	80.50	73.700	86.900	42.8	37.20	78.3
		Protein, Fat	Animal	15.0	3.40	.510	.600	78.1	.50	1.1
		Fat, Protein	<i>Pinus albicaulis</i>	5.0	.67	.030	.040	73.6	.03	.1
		Starch	Herbs	68.3	15.30	10.500	12.400	78.8	9.80	20.6
		Sugar	Shrubs, Herbs	1.6	.32	.005	.006	Unknown	----	----
		Total				100.15	84.745	99.946		47.53
September	13	Protein	Succulent Herbs	76.9	42.7	32.8	60.3	42.8	25.8	57.3
		Protein, Fat	Animal	15.4	10.0	1.5	2.8	78.1	2.2	4.9
		Fat, Protein	<i>Pinus albicaulis</i>	46.1	16.5	7.6	14.0	73.6	10.3	22.9
		Starch	Herbs	46.1	10.0	4.6	8.5	78.8	6.7	14.9
		Sugar	Shrubs, Herbs	38.5	20.7	7.9	14.5	Unknown	----	----
		Total				99.9	54.4	100.1		45.0
October	4	Fat, Protein	<i>Pinus albicaulis</i>	74.0	75.0	55.5	89.8	73.6	66.1	89.2
		Starch	Herbs	25.0	25.0	6.3	10.2	78.8	8.0	10.8
		Total				100.0	61.8	100.0		74.1
Annual Summary										
	133	Protein	Succulent Herbs	89.5	71.6	64.10	82.20	42.8	35.2	71.7
		Protein, Fat	Animal	15.0	3.9	.59	.76	78.1	.6	1.2
		Fat, Protein	<i>Pinus albicaulis</i>	9.0	4.2	.38	.49	73.6	.4	.8
		Starch	Herbs	70.7	18.1	12.80	16.40	78.8	12.9	26.3
		Sugar	Shrubs, Herbs	4.5	2.2	.10	.13	Unknown	----	----
		Total				100.0	77.97	99.98		49.1

and protein and fat from animal material contributed 1.2 percent.

Table 39 and Figures 20 and 21 present 1974 seasonal grizzly nutrient intake and nutritive values for the lake economy. The largest sample was taken in July, the time of greatest feeding activity in the economy. In July, nutritive value percents of protein from succulent herbs and protein and fat from fish were roughly similar with respective values of 53.3 and 45.1. In the annual summaries of nutritive value percents, protein from succulent herbs contributed 53.9 percent of the grizzly's energy intake, protein and fat from fish contributed 44.6 percent and starch contributed 1.5 percent.

Table 40 and Figure 22 present comparisons among economies of nutrient intake and nutritive values for 1973-1974 and a two-year parkwide summary of nutrient intake and nutritive values. Each economy appears to have had a nutritional plane distinct from the others (Table 40). In the valley/plateau economy primary nutritive value percents were 78.5 for protein from succulent herbs, 15.2 for protein and fat from animal material and 6.2 for starch. In the mountain economy, primary nutritive value percents were 69.9 for protein from succulent herbs and 26.9 for starch. In the lake economy primary nutritive value percents were 58.4 for protein from succulent herbs and 41.6 for protein and fat from fish. Protein from succulent herbs appeared to be the primary and sustaining nutrient in all three economies. The valley/plateau economy is nutritionally distinguished

TABLE 39. 1974 SEASONAL GRIZZLY BEAR NUTRIENT INTAKE AND NUTRITIVE VALUES - LAKE ECONOMY.

Month	Scat Sample	Principal Nutrient	Source	Frequency of Occurrence Percent	Percent of Diet Volume	Importance Value	Importance Value Percent	Apparent Digestibility Percent	Nutritive Value Index Percent	
June	3	Protein	Succulent Herbs	66.6	50.0	33.3	50.0	42.8	21.4	35.4
		Protein, Fat	Animal	66.6	50.0	33.3	50.0	78.1	39.1	64.6
Total					100.0	66.6	100.0		60.5	100.0
July	76	Protein	Succulent Herbs	93.4	56.5	52.80	67.40	42.8	28.80	53.3
		Protein, Fat	Animal	71.0	35.9	24.50	31.30	78.1	24.40	45.1
		Starch	Herbs	18.4	4.7	.87	1.10	78.8	.87	1.6
		Sugar	Shrubs, Herbs	5.3	2.9	.15	.20	Unknown	-----	-----
Total					100.0	78.32	100.00		54.07	100.0
August	4	Protein	Succulent Herbs	75.0	79.9	59.9	85.7	42.8	36.7	76.6
		Protein, Fat	Animal	50.0	20.0	10.0	14.3	78.1	11.2	23.4
Total					99.9	69.9	100.0		47.9	100.0
Annual Summary										
	83	Protein	Succulent Herbs	92.7	58.5	54.20	67.90	42.8	29.1	53.9
		Protein, Fat	Animal	69.9	35.3	24.70	30.90	78.1	24.1	44.6
		Starch	Herbs	18.1	4.6	.83	1.00	78.8	.8	1.5
		Sugar	Shrubs, Herbs	4.8	2.7	.13	.16	Unknown	-----	-----
Total					101.1	79.86	99.96		54.0	100.0

TABLE 40. NUTRIENT INTAKE AND NUTRITIVE VALUE COMPARISON AMONG ECONOMIES AND PARKWIDE SUMMARY - 1973-1974.

Principal Nutrient	Source	Valley/Plateau Economy Scat Sample - 340		Mountain Economy Scat Sample - 170		Lake Economy Scat Sample - 105		Parkwide Scat Sample - 615	
		Importance Value Percent	Nutritive Value Percent	Importance Value Percent	Nutritive Value Percent	Importance Value Percent	Nutritive Value Percent	Importance Value Percent	Nutritive Value Percent
Protein	Succulent Herbs	85.90	78.50	80.81	69.9	71.400	58.40	85.80	77.30
Protein, Fat	Animal	9.10	15.20	.91	1.4	27.900	41.60	8.10	13.30
Fat, Protein	<i>Pinus albicaulis</i>	.08	.13	1.20	1.8			.21	.32
Starch	Herbs	3.70	6.20	16.90	26.9	.006	.01	5.50	9.10
Sugar	Shrubs, Herbs	.53	Unknown	.11	Unknown	.001	Unknown	.30	Unknown
Total		99.31	100.03	99.92	100.0	99.307	100.01	99.91	100.02

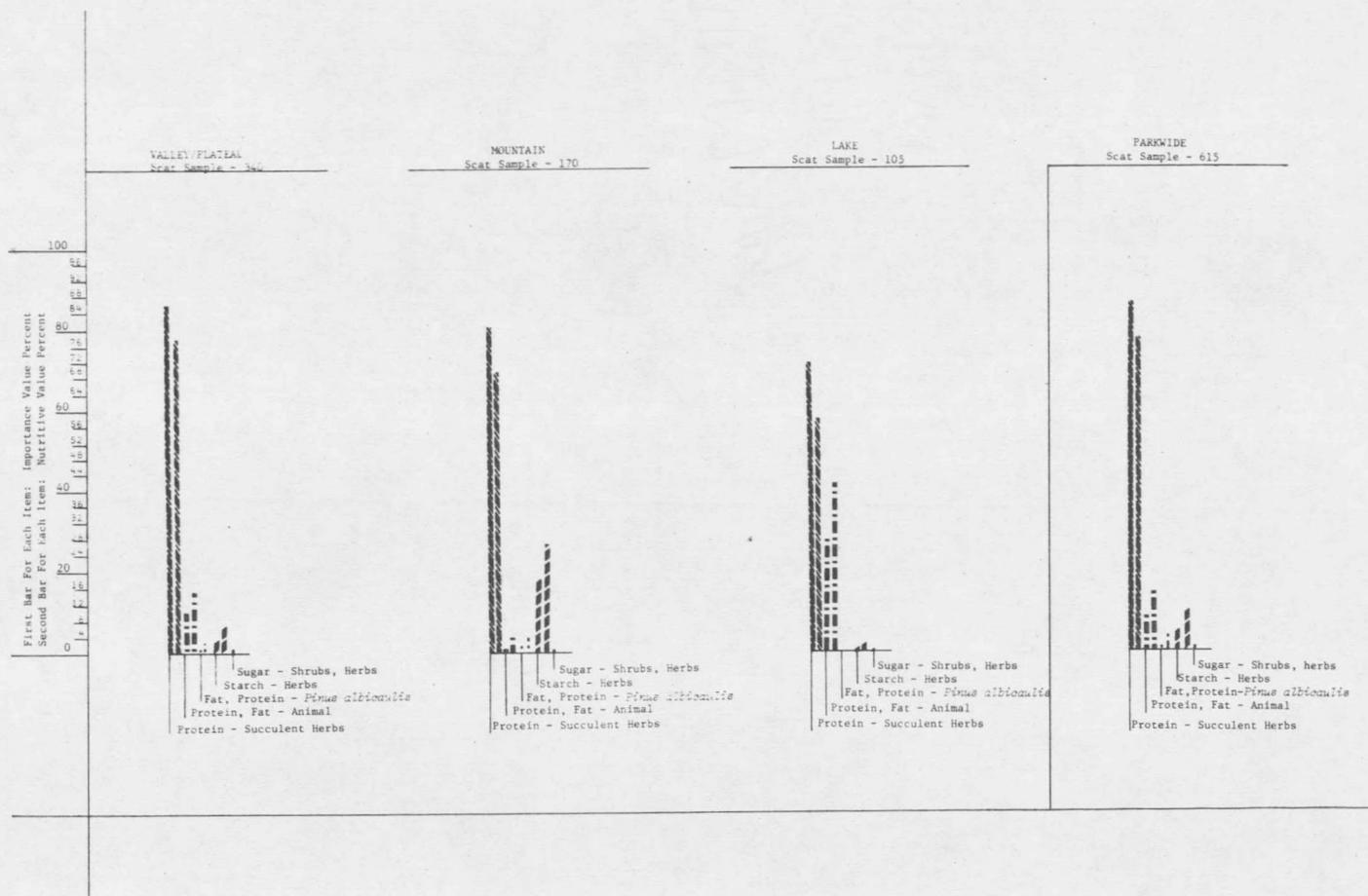


Figure 22. Nutrient importance value and nutritive value comparisons among Yellowstone National Park grizzly bear food economies and parkwide summary, 1973-1974.

by the relatively high nutritive value percent of protein from succulent herbs. The mountain economy is distinguished by the relatively high nutritive value percent of starch and the lake economy is distinguished by the relatively high nutritive value percent of protein and fat from fish.

The parkwide summaries in Table 40 and Figure 22 show that protein from succulent herbs, with a nutritive value percent of 77.3, was the grizzly's most important source of energy. Protein and fat from animal material ranked second in energy contribution importance with a nutritive value percent of 13.3. Starch ranked third with a nutritive value percent of 9.1 and fat and protein from whitebark pine nuts ranked fourth with a nutritive value percent of 0.32. Energy contribution of sugar from fruits and berries is unknown, but it is unlikely that its nutritive value percent would have exceeded 0.50.

In Table 40 and Figure 22, protein from succulent herbs had a nutritive value percent lower than its importance value percent because its digestibility was lower relative to that of the principal nutrient materials from other sources. Starch, protein and fat from animal material, and fat and protein from whitebark pine nuts had nutritive value percents higher than their importance value percents because their respective digestibilities were high relative to that of protein from succulent herbs.

Plant Protein/Succulence-Flowering Relationships

Table 41 presents the relationships between plant protein and succulence-flowering condition in herbs. In sample plots 1-3, protein levels were highest when plants were succulent and in either pre-flowering or flowering status. Protein levels were lowest when plants were in post-flowering status and either drying or desiccated. In all three plots there was an inverse relationship between protein and crude fiber levels. In plots 4 and 5, high protein levels appeared to be directly related to succulence since flowering had been completed in all samples. Protein Loss Factor data (Table 41) show protein depletion for the samples which probably resulted from drying and completion of reproduction. This was expected because protein is primarily a constituent of active tissues, especially the reproductive parts (Marnard and Loosli, 1969). Grizzlies appeared to be automatically linked to the highest source of herbaceous protein available by feeding on herbs in their most succulent condition.

Distribution and Physiography

Figure 23 presents data showing grizzly distribution by economy (Figure 5) combined with data reflecting the Park's three physiographic/vegetative units (Figure 4). Grizzly feeding economies appeared to be directly correlated with soil fertility. Economies were centered on areas with fertile soils; little feeding activity was

TABLE 41. PLANT PROTEIN/SUCCULENCE-FLOWERING RELATIONSHIP - 1974.

Sample Plot	Food Item	Economy	Date	Condition	Percent Protein	Percent Crude Fiber	Protein Loss Factor*
1	<i>Agropyron</i> sp. - 50%, <i>Poa</i> sp. - 20%, <i>Bromus</i> sp. - 10%, <i>Phleum alpinum</i> - 10%, <i>Carex</i> sp. - 10%	Mountain	7/20	Pre-flowering, Succulent	22.9	26.2	7.3
			8/26	Post-flowering, Drying	12.4	27.1	
			9/29	Post-flowering, Dessicated	4.7	39.4	
2	<i>Trifolium parryi</i>	Mountain	7/20	Flowering, Succulent	21.0	14.8	2.6
			8/25	Post-flowering, Drying	11.1	20.3	
3	<i>Deschampsia atropurpurea</i> - 40%, <i>Poa</i> sp. - 40%, <i>Carex</i> sp. - 20%	Valley/Plateau	7/11	Pre-flowering, Succulent	13.2	27.8	1.5
			8/10	Flowering, Succulent	13.9	25.6	
			9/3	Post-flowering, Drying	9.2	28.4	
4	<i>Calamagrostis inexpansa</i>	Valley/Plateau	9/2	Post-flowering, Succulent	16.3	24.7	5.1
			9/2	Post-flowering, Dessicated	4.1	30.7	
5	<i>Poa</i> sp.	Valley/Plateau	10/2	Post-flowering, Succulent	17.4	11.4	13.6
			10/2	Post-flowering, Dessicated	4.0	37.3	

*Early $\frac{\% \text{ Protein}}{\% \text{ Crude Fiber}} = \text{PLF}$
 Late $\frac{\% \text{ Protein}}{\% \text{ Crude Fiber}}$

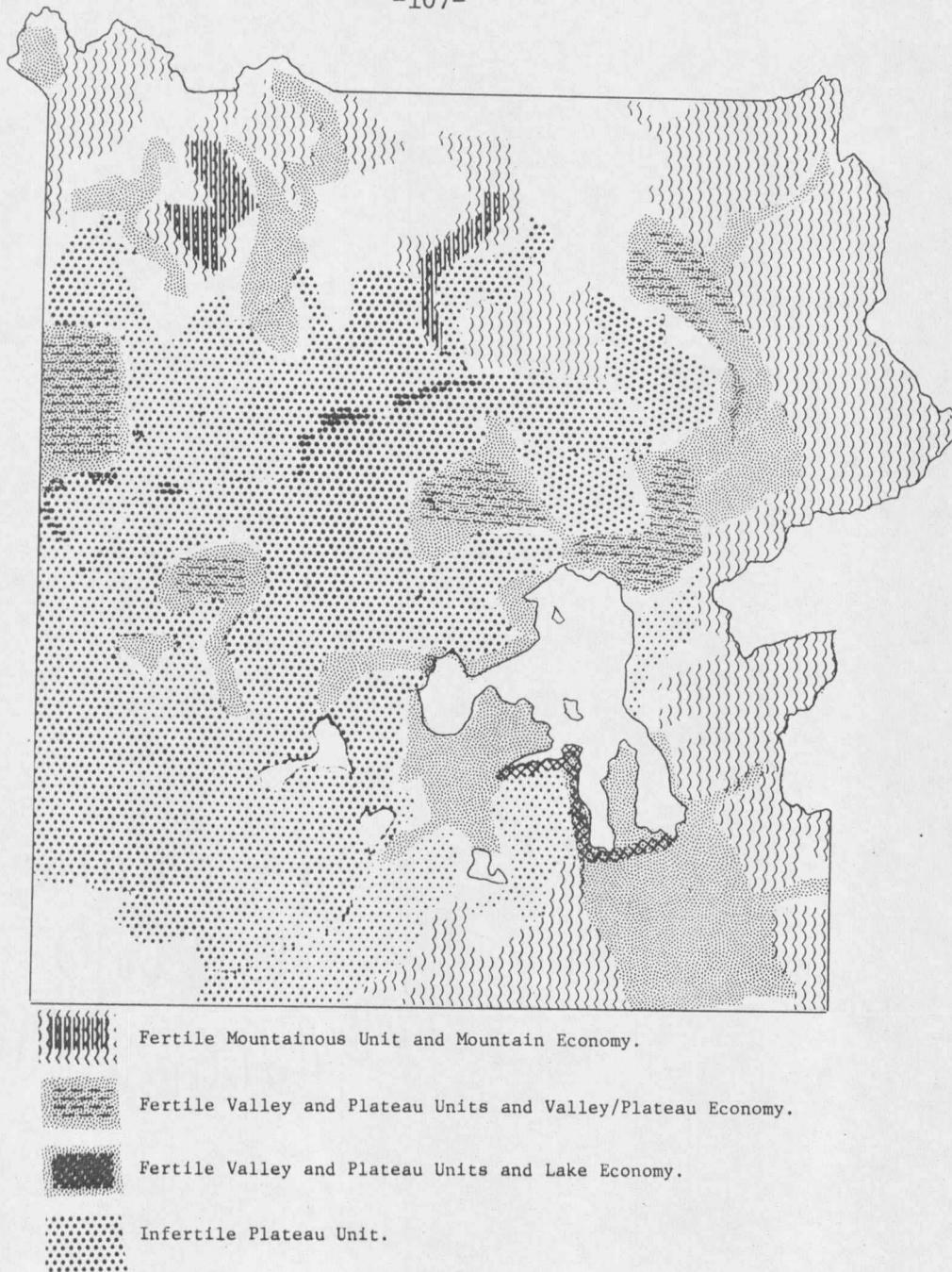


Figure 23. Map showing grizzly distribution by food economy superimposed over the Park's physiographic/vegetative units.

apparent on infertile soils. Highest grizzly densities, excluding the lake economy, were reported on the rich grasslands of Hayden and Pelican Valleys (Knight, 1975). Similar relationships between soils and wildlife were pointed out by Crawford (1950). Macpherson (1965) pointed out a positive correlation between the occurrence of Barren-Ground Grizzly Bears and sedimentary basins and youthful folded mountain ranges.

Of the two physiographic units in the Park with fertile soils, the valley and plateau unit appears to be the largest. Because of its relative size and the fact that it has a high reported bear density, this unit probably supports a higher total number of bears than the mountainous unit.

Grizzly Bear Anatomy

Table 42 presents intestinal lengths of two Yellowstone grizzlies and two non-Yellowstone black bears. The fresh carcass of grizzly #1 was obtained September 20, 1974, and the fresh carcass of grizzly #2 was obtained November 11, 1974. The fresh carcasses of the two black bears were obtained in August 1974. how?

The total intestine length of grizzly #1 was 984.5 cm. and the ratio of intestine to head and body length was 7.4/1. The small intestine was 15 times longer than the colon and rectum. Grizzly #2 had a total intestine length of 769.2 cm. and a 4.3/1 ratio of

TABLE 42. INTESTINAL LENGTH IN GRIZZLY AND BLACK BEARS.

	Grizzly #1	Grizzly #2	Black Bear #1	Black Bear #2
Age	1.5 years	"old"	Adult	Adult
Weight	47.6 kg.	113.6 kg. (est.)	136.8 kg.	95.5 kg.
Head and body length	133.3 cm.	200 cm.	187.1 cm.	194.9 cm.
Length small intestine	923.0 cm.	769.2 cm.	771.8 cm.	Unknown
Length colon and rectum	61.5 cm.	94.9 cm.	53.8 cm.	Unknown
Total length intestine	984.5 cm.	864.1 cm.	825.6	1138.4
<u>Intestine</u> Head and Body	7.4	4.3	4.4	5.8

intestine to head and body length. The small intestine was 8 times the length of the colon and rectum. The ratio of intestine to head and body length of black bears #1 and #2 were 4.4, and 5.8, respectively. The ratio of grizzly #1 is comparable to that reported for *Ursus arctos* by Davis (1964); the ratio for grizzly #2 is much lower than that reported by Davis. Davis (1964) reported intestine to head and body ratios for *Ursus americanus* of 6.8/1 and 7.4/1. The black bear ratios in Table 42 are lower.

Davis (1964) notes a broad correlation between gut length and diet in carnivores. Exclusively meat eating carnivores such as the Canidae were found to have lower intestine to head and body length ratios than

the mixed diet carnivores such as the Ursidae. Davis stated that bears were the most herbivorous of the carnivores and had the greatest gut length. My data do not seriously conflict with Davis' conclusions with respect to grizzly gut length and diet.

The simple stomachs and intestines of grizzlies #1 and #2 were dissected and grossly examined. The stomach of grizzly #2 measured 66.6 cm. around the greater curvature, the fundus was 47.4 cm. and the pylorus 19.2 cm. Fully distended stomach capacity was 2,600 ml. The fundus was thin-walled, the rugae were covered with scarlet tissue. The pylorus had thick muscular walls, the rugae were covered with yellow tissue. The stomach of grizzly #1 measured 76.9 cm. around the greater curvature, the fundus was 48.7 cm. and the pylorus was 28.2 cm. Fully distended stomach capacity was 950 ml. No caecum were present in the digestive tracts.

Yampa residues were recovered from the stomach and duodenum of grizzly #1. Starch analysis of the stomach residue showed the material to have a 43 percent starch content, while starch analysis of the intestinal residue indicated a 14 percent starch content. This data reveals the duodenum as the probable site for primary starch digestion, and also shows a higher starch digestibility for yampa (65.1 percent) than is indicated in Table 28.

The data suggests that the digestive physiology of the grizzly represents adaptations to a heavily herbivorous diet; such adaptations

do not appear to impair the capacity to assimilate animal food material with a high degree of efficiency.

DISCUSSION

The Ursidae evolved from the Canidae during the Miocene Epoch (Colbert, 1969; Herrero, 1972). Grizzlies were present by the middle Pleistocene and probably occupied open tundra areas left bare by retreating ice during the interglacials (Herrero, 1972). During the last ten thousand years, grizzlies extended their range into the interior of North America where they probably occupied the edge and river bottoms of the great plains; buffalo carrion, supplemented with occasional kills, and a steady availability of grasses and forbs probably served as high quality foods for grizzlies (Herrero, 1972).

The postulated pattern of habitat use and food consumption by prehistoric grizzlies in the great plains appears to be reflected in Yellowstone Park. In the Park, grizzlies appeared to occupy primarily fertile, open grasslands where protein, provided by succulent herbs and secondarily by artiodactyls, apparently served most of the grizzly's energy needs (Table 40). Because of its nutritional dependence on protein, the Yellowstone grizzly in 1973-1974 appeared to occupy primarily a protein food niche. Protein, taken from plant and animal sources in large quantities, apparently provided for grizzly protein needs and energy needs as well. This was possible 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).

In this study, Park grizzlies were seen to graze for long periods in grasslands. Protein digestibility of grassland herbs was reported as 42.8 percent (Table 36). This was considerably lower than the indicated digestibilities of the other principal nutrient materials. Apparently Park grizzlies compensated for this relatively low nutrient digestibility by a high intake of succulent herbs which insured a high level of ingested protein, and a consequent energy source and fat store. Geist (1974) noted a similar process in the perissodactyl who can "compensate for poor forage of low digestibility by eating more and passing 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 the dentition of the Ursidae and Hoffmann and Pattie (1968) and Greer and Craig (1971) have 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. This is an apparent adaptation to a herbivorous or omnivorous diet. The front claws of the grizzly are greater than 55 mm. allowing the grizzly to be an effective digger, possibly an additional adaptation to herbivory. The Yellowstone grizzly's occupation of its

primarily plant protein food niche is attributable in part to its gut length, bunodont molars and long claws. These physical characteristics allowed utilization of plant materials without preventing a high digestibility (78.1 percent, Table 36) of animal material. As a result, grizzlies appeared to be digestively flexible and seemed able to make maximum use of protein available from plant and animal sources. Such digestive flexibility probably accounted in part for the apparently successful exploitation of the Park's three different food economies.

The Yellowstone grizzly appeared to be adapted primarily to the most constant and abundant protein sources in its environment: succulent herbs and animal material from open, fertile grasslands. Fertile grasslands were the sites of constant protein supply because a relatively large portion of light energy fixed by photosynthesis was available as food energy directly in herbs and indirectly in herbivores. Coniferous forests did not provide a constant protein source for grizzlies because most of the absorbed light energy was in the forest canopy and unavailable as food. In 1974, seasonal foods such as pine nuts and berries were relatively abundant and contributed 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 had no major impact on Park grizzlies because nutritionally they were probably

anchored to the more stable energy supply available from fertile grasslands and associated forested edges.

The animal (artiodactyl) sources of protein from open areas probably have been less constant in availability than the plant sources. Relative scarcity of artiodactyl food material during the pre-green-up period has probably meant an absolute limit of protein availability to grizzlies during this time. Such a limit could have had a limiting effect on grizzly numbers when their demand for animal protein has exceeded the supply. In such cases, competition among grizzlies for animal material may have occurred (Cole, 1972) and resulted in population losses. Probable losses may have occurred among subordinate bears through dispersal and direct mortality (Stokes, 1970; Martinka, 1974). The pre-growing season appears to be the only time in the Park when absolute limits on protein available to the bears could have existed. This period is likely to be the primary one in which natural grizzly population regulation has occurred.

The grizzly population in the Park has been estimated to be 178-270 and the highest density, excluding the Yellowstone Lake area, has been estimated to be 2.2 ^{3 KH2} m²/bear 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 apparently have been secondary consumers during pre-green-up periods and probably, during these periods, have been subject to population limitation at levels set by the amounts of available animal protein.
- 2) Grizzlies have been relatively inefficient grazers because of their dentition and digestive structure. Because of this inefficiency, they must have required tall, dense stands of succulent, protein rich herbs. The available supply of such areas probably has had a limiting effect on grizzly numbers.

As indicated earlier, grizzlies appeared to graze with their heads perpendicular to the forage and pluck the vegetation by grasping it in their molars. They did not appear capable of cropping vegetation close as artiodactyls do, instead they appeared to require relatively tall (8 cm.) and dense stands of herbs in order to graze efficiently.

Grizzly digestive capability with respect to succulent herbs appeared to be 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/gram of vegetation than grizzlies. In order to maximize energy intake and compensate for low energy/gram forage utilization, grizzlies appeared to seek out and ingest large quantities of succulent herbs growing in

tall, dense stands. Such high quality stands were extensive in the Park but not unlimited. They were also preferred by elk and bison.

Free-ranging grizzly bears in Yellowstone Park using natural foods occupied a multi and mixed level trophic niche in 1973-1974. The niche was adapted to the constant availability of protein from succulent herbs and artiodactyls in fertile, open grasslands. The grizzly maintained the niche because of its digestive flexibility which permitted maximum protein use of plant and/or animal material.

The essential environmental requirement necessary to support grizzlies on a continuing basis in this niche appeared to be the availability of fertile grasslands capable of maintaining elk and bison in sufficient numbers to provide adequate food for pre-green-up secondary consumption, rodents for growing season mixed consumption, and tall, dense, succulent and nutritious herbs in sufficient amounts for growing and post-growing season primary and mixed consumption.

SUMMARY AND CONCLUSIONS

1) The concept that Park grizzlies were distributed in three physiographically distinct food economies served as a working hypothesis for the study. An economy was defined as a distinctive mix of physiographic and biotic conditions which resulted in a characteristic pattern of interactions between grizzlies and food items unique to each economy. Data resulting from the research supported the existence of three economies: the valley/plateau, mountain and lake economies.

2) The valley/plateau economy was centered primarily on the open grasslands of fertile, transported valley soils surrounded by infertile plateau soils with lodgepole pine forests; the mountain economy was centered on fertile andesitic and sedimentary derived soils supporting nutritious, herbaceous plant growth in mountain meadows and on ridgetops; the lake economy was centered on Yellowstone Lake tributaries containing spawning cutthroat trout. Each economy appeared to have unique food consumption patterns: the valley/plateau economy was primarily a grass/rodent economy and grizzlies were intensive diggers; the mountain economy was primarily a grass/springbeauty/root economy and grizzlies were casual diggers; the lake economy was primarily a fish/grass economy and grizzlies were fishers.

3) The general feeding cycle in the valley/plateau and mountain economies appeared to follow plant phenology. During the pre-growing season, grizzlies were primarily meat eaters. During the growing and post-growing seasons, grizzlies ate primarily succulent herbs although meat, corms and berries became important items during the post-growing season in the valley/plateau economy, and pine nuts became important in the mountain economy.

4) Distribution of bears in the valley/plateau and mountain economies was primarily influenced by plant moisture conditions. Bears concentrated on sites with succulent herbs.

5) Succulent grasses and sedges, with an importance value percent of 78.5, were the most important items consumed as food by grizzlies in the Park in 1973-1974. Grazing on these items was concentrated in dense stands of succulent forage at least 8 cm. tall. Grazing sessions of individual grizzlies were intense and lengthy.

6) Digestibility of pre- and post-flowering herbs suggested a digestive flexibility in grizzlies which may have provided a relatively constant energy intake regardless of changes in diet levels of protein and nitrogen-free extract.

7) Protein from animal tissue was more digestible than protein from plant tissue. In plants, storage fats were more digestible than structural fats.

8) Food energy and digestibility were directly related: the higher the food energy, the greater its digestibility.

9) Five principal materials contributing to total grizzly energy intake and their sources and digestibilities were identified. Protein from succulent herbs had an estimated digestibility of 42.8 percent, protein and fat from animal material had an estimated digestibility of 78.1 percent, fat and protein from pine nuts had an estimated digestibility of 73.6 percent, starch from herbs had an estimated digestibility of 78.8 percent, and the digestibility of sugar from berries and fruits of shrubs and herbs was not determined.

10) In the valley/plateau economy in 1974, the principal energy source during the pre-growing season was protein and fat from elk. Protein from succulent herbs was the principal energy source during the growing and post-growing seasons. In the mountain economy, the principal energy source during the pre-growing season was suspected to be protein from elk and moose. Protein from succulent herbs and starch were the key energy providing nutrients during the growing and post-growing seasons. Protein and fat from fish and protein from succulent herbs provided energy to grizzlies in the lake economy.

11) Each of the three economies appeared to have had a nutritional plane distinct from the others; protein from succulent herbs was the primary nutrient in the valley/plateau economy, protein from succulent herbs and starch were the principal nutrients in the mountain

economy and protein and fat from fish and protein from succulent herbs were the primary nutrients in the lake economy.

12) Protein from succulent herbs, with a nutritive value percent of 77.3 was the grizzly's most important energy source in the Park in 1973-1974.

13) Succulent, pre-flowering herbs had higher protein levels than dry, mature herbs; grizzly use of succulent herbs guaranteed them the highest source of herbaceous protein available.

14) Grizzly feeding economies in the Park were directly correlated with soil fertility.

15) The digestive physiology of the grizzly represents an adaptation to a heavily herbivorous diet; such adaptations do not impair the capacity to assimilate animal food material with a high degree of efficiency.

16) The Yellowstone grizzly in 1973-1974 appeared to occupy primarily a protein food niche. Protein provided for both protein and energy requirements because protein is convertible to fat and ketone bodies via the intermediary metabolism and such conversion occurs especially when protein is taken in excess.

17) Park grizzlies apparently compensated for relatively low protein digestibility of succulent herbs by high intake which insured an excess of ingested protein and a consequent energy source and fat store.

18) Grizzlies appeared to be digestively flexible and seemed able to make maximum use of protein from plant and animal sources. Such flexibility probably accounted for the apparently successful exploitation of the Park's three different food economies.

19) The Yellowstone grizzly appeared to be adapted primarily to the most constant and abundant protein sources in its environment: succulent herbs and animal material from open fertile grasslands.

20) Competition among grizzlies during the pre-growing season for animal food material (primarily elk) could have had regulatory consequences for the grizzly population.

21) The grizzly population level and densities in the Park can be partially accounted for by the apparent facts that grizzlies are secondary consumers during pre-green-up periods and that they are relatively inefficient primary consumers during the growing and post-growing seasons.

22) Free-ranging grizzly bears in Yellowstone Park using natural foods were primarily herbivores (primary consumers) and were secondarily in an intermediate trophic position eating mixtures of plant and animal food. The grizzly was a carnivore (secondary consumer) in the pre-growing season. Nutritionally, the grizzly was primarily a herbivore and secondarily a carnivore. The essential environmental requirement necessary to support grizzlies on a continuing basis in this niche appeared to be the availability of fertile grasslands

capable of maintaining elk and bison as food for pre-green-up secondary consumption, rodents for growing season mixed consumption and nutritious and abundant herbs for growing and post-growing season primary and mixed consumption.

APPENDIX

TABLE 43. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
AGROPYRON SP. - 50%, *POA* SP. - 20%, *BROMUS* SP. - 10%, *PHLEUM ALPINUM* - 10%,
CAREX SP. - 10%.

Item: Graminae/Cyperaceae

Importance Value Percent: 78.5

Species: *Agropyron* sp. - 50%, *Poa* sp. - 20%, *Bromus* sp. - 10%, *Phleum alpinum*
 - 10%, *Carex* sp. - 10%

Economy: Mountain

Condition: Pre-flowering, Succulent

Rank: 1

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	22.9	5.6	128.2	11.5	5.6	64.4	63.8	0	49.8
Ether Extract	3.7	9.3	34.4	4.5	9.3	Unknown	Unknown	1.2	Unknown
Fiber	26.2			31.5				1.2	
Nitrogen-free Extract	39.4	4.3	169.4	39.6	4.3	Unknown	Unknown	Unknown (1.01)*	Unknown
Ash	7.7			12.8				1.7	
Total	99.9		332.0	99.9			63.8		
Per Gram			3.3				.64		19.4
Calcium %		.35			.88			2.5	
Phosphorous %		.35			.20			0	

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 44. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

POA SP. - 50%, AGROPYRON SP. - 30%, PHLEUM ALPINUM - 10%, CAREX SP. - 10%.

Item: Graminae/Cyperaceae

Importance Value Percent: 78.5

Species: . *Poa* sp. - 50%, *Agropyron* sp. - 30%, *Phleum alpinum* - 10%,
Carex sp. - 10%

Economy: Mountain

Condition: Pre-flowering, Succulent

Rank: 1

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	25.6	5.6	143.4	13.3	5.6	74.5	68.9	0	48.0
Ether Extract	3.6	9.3	33.5	4.7	9.3	Unknown	Unknown	1.3	Unknown
Fiber	26.4			25.4				0	
Nitrogen-free Extract	35.9	4.3	154.4	38.4	4.3	Unknown	Unknown	Unknown (1.1)*	Unknown
Ash	8.5			18.2				2.1	
Total	100.0		331.3	100.0			68.9		
Per Gram			3.3				.69		20.9
Calcium %		.35			1.30			3.7	
Phosphorous %		.38			.48			1.3	
Gross Energy		1864.2			1623.9				

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 45. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

DESCHAMPSIA ATROPURPUREA - 80%, *CAREX* SP. - 10%.

Item: Graminae/Cyperaceae

Importance Value Percent: 78.5

Species: *Deschampsia atropurpurea* - 80%, *Carex* sp. - 10%

Economy: Mountain

Condition: Post-flowering, Succulent

Rank: 1

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	14.0	5.6	78.4	8.3	5.6	46.5	31.9	0	40.7
Ether Extract	2.7	9.3	25.1	3.6	9.3	Unknown	Unknown	1.1	Unknown
Fiber	29.3			24.6				0	
Nitrogen-free Extract	46.8	4.3	201.2	41.1	4.3	Unknown (176.7)*	Unknown (24.5)	0	Unknown (12.2)
Ash	7.1			22.9				3.2	
Total	99.9		304.7	99.9			31.9(56.4)		
Per Gram			3.0				.32(.56)		10.7(18.8)
Calcium %		.37			1.3			3.5	
Phosphorous %		.26			.47			1.8	
Gross Energy		1894.1			1440.5				

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 46. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

POA SP. - 100%.

Item: Graminae/Cyperaceae

Importance Value Percent: 78.5

Species: *Poa* sp. - 100%

Economy: Valley/Plateau

Condition: Post-flowering, Succulent

Rank: 1

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	17.4	5.6	97.4	11.0	5.6	61.6	35.8	0	36.7
Ether Extract	1.5	9.3	13.9	2.8	9.3	Unknown	Unknown	1.9	Unknown
Fiber	11.4			24.7				2.2	
Nitrogen-free Extract	62.2	4.3	267.5	45.0	4.3	Unknown (193.6)*	Unknown (73.9)	0	Unknown (27.6)
Ash	7.6			16.4				2.2	
Total	100.1		378.8	99.0			35.8(109.7)		
Per Gram			3.8				.36(1.1)		9.5(28.9)
Calcium %		.27							
Phosphorous %		.25							

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 47. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
CALAMAGROSTIS INEXPANSA - 100%.

Item: Graminae/Cyperaceae

Importance Value Percent: 78.5

Species: *Calamagrostis inexpansa* - 100%

Economy: Valley/Plateau

Condition: Post-flowering, Succulent

Rank: 1

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	17.6	5.6	98.6	11.5	5.6	64.4	34.2	0	34.7
Ether Extract	5.0	9.3	46.5	2.1	9.3	19.5	27.0	0	58.0
Fiber	24.6			31.4				1.3	
Nitrogen-free Extract	41.9	4.3	180.2	41.0	4.3	Unknown (176.3)*	Unknown (3.9)	0	Unknown (2.2)
Ash	10.9			14.0				1.3	
Total	100.6		325.3	100.0			61.2(65.1)		
Per Gram			3.3				.61(.65)		18.5(19.7)

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 48. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
CLAYTONIA LANCEOLATA - 100%; SAMPLE #1.

Item: *Claytonia lanceolata*

Importance Value Percent: 6.1

Species: Same - 100%

Economy: Mountain

Condition: Pre-flowering, Succulent, Entire

Rank: 2

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	30.0	5.6	168.0	10.0	5.6	56.0	112.0	0	67.0
Ether Extract	2.8	9.3	26.0	5.7	9.3	53.0	Unknown	2.0	Unknown
Fiber	10.9			20.2				1.9	
Nitrogen-free Extract:									
Starch	11.3		48.6	.8		3.4*	45.2	0	93.0
Non-Starch	36.9	4.3	158.7	37.1	4.3	Unknown (159.5)**	Unknown	Unknown (1.005)	Unknown
Ash	8.2			26.2				3.2	
Total	100.1		401.3	100.0			157.2		
Per Gram			4.0				1.6		40.0

*Starch values determined by direct, starch-specific analysis.

**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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 49. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
 CLAYTONIA LANCEOLATA - 100%, SAMPLE #2.

Item: *Claytonia lanceolata*

Importance Value Percent: 6.1

Species: Same - 100%

Economy: Mountain

Condition: Pre-flowering, Succulent, Above Ground

Rank: 2

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	39.0	5.6	218.4	12.1	5.6	67.8	150.6	0	69.0
Ether Extract	3.6	9.3	33.5	6.9	9.3	64.2	Unknown	1.9	Unknown
Fiber	10.0			24.8				2.5	
Nitrogen-free Extract	38.1	4.3	163.8	40.7	4.3	Unknown (175.0)*	Unknown	Unknown (1.1)	Unknown
Ash	9.3			15.4				1.7	
Total	100.0		415.7	99.9			150.6		
Per Gram			4.2				1.5		35.7
Calcium %					1.38				
Phosphorous %					.35				
Gross Energy					1820.5				

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 50. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
CLAYTONIA LANCEOLATA - 100%, SAMPLE #3.

Item: *Claytonia lanceolata*

Importance Value Percent: 6.1

Species: Same - 100%

Economy: Mountain

Condition: Flowering, Succulent, Above Ground

Rank: 2

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	20.7	5.6	115.9	10.5	5.6	58.8	57.1	0	49.3
Ether Extract	5.4	9.3	50.2	6.5	9.3	60.5	Unknown	1.2	Unknown
Fiber	12.0			23.6				2.0	
Nitrogen-free Extract	50.8	4.3	218.4	39.3	4.3	Unknown (169.0)*	Unknown (49.4)	0	Unknown (22.6)
Ash	<u>11.1</u>			<u>20.1</u>				<u>1.8</u>	
Total	100.0		384.5	100.0			57.1(106.5)		
Per Gram			3.8				.6(1.1)		15.8(28.9)
Calcium %					1.65				
Phosphorous %					.46				
Gross Energy					1788.0				

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 51. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

TRIFOLIUM REPENS - 100%, SAMPLE #1.

Item: *Trifolium repens*

Importance Value Percent: 2.4

Species: Same - 100%

Economy: Valley/Plateau

Condition: Flowering, Succulent

Rank: 4

	Whole Food Material			Corresponding Scat Material					
	Proxi- ment Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	22.0	5.6	123.2	13.8	5.6	77.3	45.9	0	37.3
Ether Extract	3.0	9.3	27.9	1.8	9.3	16.7	11.2	0	40.1
Fiber	17.4			26.7				1.5	
Nitrogen-free Extract	47.5	4.3	204.3	44.1	4.3	Unknown (189.6)*	Unknown (14.7)	0	Unknown (7.2)
Ash	<u>10.0</u>			<u>13.4</u>				1.3	
Total	99.9		355.4	99.8			57.1(71.8)		
Per Gram			3.6				.57(.72)		15.8(20.0)
Calcium %		2.43							
Phosphorous %		.26							

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 52. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

TRIFOLIUM REPENS - 100%, SAMPLE #2.

Item: *Trifolium repens*

Importance Value Percent: 2.4

Species: Same - 100%

Economy: Valley/Plateau

Condition: Flowering, Succulent

Rank: 4

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	23.1	5.6	129.4	16.1	5.6	90.2	39.2	0	30.3
Ether Extract	2.8	9.3	26.0	2.4	9.3	22.3	3.7	0	14.2
Fiber	15.8			25.8				1.6	
Nitrogen-free Extract	47.2	4.3	202.9	37.0	4.3	Unknown (159.1)*	Unknown (43.8)	0	Unknown (21.6)
Ash	11.2			18.6				1.6	
Total	100.1		358.3	99.9			42.9(86.7)		
Per Gram			3.6				.43(.87)		11.9(24.4)
Calcium %		1.63							
Phosphorous %		.25							

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 53. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

SALMO CLARKI - 100%, SAMPLE #1.

Item: *Salmo clarki*

Importance Value Percent: 1.7

Species: Same - 100%

Economy: Lake

Condition: Without Eggs

Rank: 5

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	78.60	5.6	440.2	15.7	5.6	87.9	352.3	0	80.0
Ether Extract	8.20	9.3	76.3	1.4	9.3	13.0	63.3	0	82.9
Fiber	.22			2.5				11.4	
Ash	13.00			77.6				5.9	
Total	100.02		516.5	97.2			415.6		
Per Gram			5.2				4.2		80.8
Calcium %		3.08			23.33			7.6	
Phosphorous %		2.25			10.88			4.8	
Gross Energy		2145.9			Fecal Energy 694.5				

TABLE 54. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

SALMO CLARKI - 100%, SAMPLE #2.

Item: *Salmo clarki*

Importance Value Percent: 1.7

Species: Same - 100%

Economy: Lake

Condition: With Eggs

Rank: 5

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	69.70	5.6	390.3	28.0	5.6	156.8	233.5	0	59.8
Ether Extract	23.00	9.3	213.9	1.6	9.3	14.9	199.0	0	93.0
Fiber	.16			3.3				20.6	
Nitrogen-free Extract	1.00	4.3	4.3	6.3	4.3	Unknown	Unknown	6.3*	Unknown
Ash	<u>6.00</u>			<u>60.7</u>				10.1	
Total	99.86		608.5	99.9			432.5		
Per Gram			6.1				4.3		70.5

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 55. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

SALMO CLARKI EGGS - 100%.

Item: *Salmo clarki*

Importance Value Percent: 1.7

Species: Eggs - 100%

Economy: Lake

Rank: 5

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	68.50	5.6	383.6	18.6	5.6	104.2	279.4	0	72.8
Ether Extract	14.60	9.3	135.8	2.9	9.3	26.9	108.9	0	80.2
Fiber	.11			16.2				147.3	
Nitrogen-free Extract	12.00	4.3	51.6	9.1	4.3	Unknown (39.1)*	Unknown (12.5)	0	Unknown (24.2)
Ash	4.80			53.2				11.1	
Total	100.01		571.0	100.0			388.3(400.8)		
Per Gram			5.7				3.9(4.0)		68.4(70.3)
Calcium %		.09			3.68			40.8	
Phosphorous %		.79			2.67			3.7	
Gross Energy		2822.6		Fecal Energy	1068.7				

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 56. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

LOMATIUM COUS ROOTS - 100%.

Item: Umbelliferae

Importance Value Percent: 1.7

Species: *Lomatium cous* roots

Economy: Mountain

Condition: Flowering

Rank: 6

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	6.0	5.6	33.6	3.9	5.6	21.8	11.8	0	35.0
Ether Extract	1.4	9.3	13.0	.8	9.3	7.4	5.6	0	43.0
Fiber	9.1			21.8				2.4	
Nitrogen-free Extract:									
Starch	34.3		147.5	.9		3.9*	143.6	0	97.4
Non-Starch	43.3	4.3	186.2	25.4	4.3	Unknown** (109.2)	Unknown (77.0)	0	Unknown (41.5)
Ash	5.9			47.3				8.0	
Total	100.0		380.3	100.1			161.0(238.0)		
Per Gram			3.8				1.6(2.4)		42.1(63.1)
Calcium %		.29							
Phosphorous %		.24							
Gross Energy		1732.5							

*Starch values determined by direct, starch-specific analysis.

**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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 57. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
PERIDERIDIA GAIRDNERI ROOTS - 100%.

Item: Umbelliferae
 Importance Value Percent: 1.7
 Species: *Perideridia gairdneri* roots - 100%
 Economy: Valley/Plateau
 Condition: Flowering
 Rank: 6

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	4.8	5.6	26.9	4.0	5.6	22.4	4.5	0	16.7
Ether Extract	.5	9.3	4.7	1.0	9.3	9.3	Unknown	2.0	Unknown
Fiber	4.0			21.0				5.3	
Nitrogen-free Extract:									
Starch	40.1		172.4	17.0		73.1*	99.3	0	57.6
Non-Starch	47.5	4.3	204.3	42.6	4.3	Unknown** (183.2)	Unknown (21.1)	0	Unknown (10.3)
Ash	3.2			14.4				4.5	
Total	100.1		408.3	100.0				103.8(124.9)	
Per Gram			4.1					1.0(1.2)	24.4(29.3)
Calcium %		.094							
Phosphorous %		.17							
Gross Energy		1816.1							

*Starch values determined by direct, starch-specific analysis.

**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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 58. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
CERVUS CANADENSIS - 100%, SAMPLE #1.

Item: Cervidae/Bovidae
 Importance Value Percent: 1.3
 Species: *Cervus canadensis* - 100%
 Economy: Valley/Plateau
 Condition: Lean Tissue
 Rank: 8

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	88.20	5.6	493.8	14.20	5.6	79.5	414.4	0	83.9
Ether Extract	6.70	9.3	62.3	.85	9.3	7.9	54.4	0	87.3
Fiber	.43			6.60				15.3	
Nitrogen-free Extract	.11	4.3	.47	17.80	4.3	Unknown	Unknown	161.8*	Unknown
Ash	<u>4.50</u>			<u>60.50</u>				13.4	
Total	99.94		556.7	99.95			468.8		
Per Gram			5.6				4.7		83.9
Calcium %		.13			14.36			110.5	
Phosphorous %		.65			.60			0	
Gross Energy		2289.2		Fecal Energy	871.8				

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 59. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

CERVUS CANADENSIS - 100%, SAMPLE #2.

Item: Cervidae/Bovidae

Importance Value Percent: 1.3

Species: *Cervus canadensis* - 100%

Economy: Valley/Plateau

Condition: Lean Tissue

Rank: 8

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	88.20	5.6	493.8	15.9	5.6	89.0	404.8	0	81.9
Ether Extract	6.70	9.3	62.3	2.5	9.3	23.3	39.0	0	62.6
Fiber	.43			2.5				5.8	
Nitrogen-free Extract	.11	4.3	.47	12.3	4.3	Unknown	Unknown	111.8*	Unknown
Ash	4.50			66.7				14.8	
Total	99.94		556.7	99.9			443.8		
Per Gram			5.6				4.4		78.6
Calcium %		.13							
Phosphorous %		.65							
Gross Energy		2289.2							

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 60. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS;

MELICA SPECTABILIS CORMS - 100%.

Item: *Melica spectabilis*

Importance Value Percent:

Species: Same - corms - 100%

Economy: Valley/Plateau

Condition: Flowering

Rank: 9

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	6.1	5.6	34.2	3.7	5.6	20.7	13.5	0	39.5
Ether Extract	.4	9.3	3.7	.2	9.3	1.9	1.8	0	48.6
Fiber	3.6			5.7				1.6	
Nitrogen-free Extract:									
Starch	10.4		44.7	3.4		14.6*	30.1	0	67.3
Non-Starch	78.3	4.3	336.7	71.3	4.3	Unknown** (306.6)	Unknown (30.1)	0	Unknown (8.9)
Ash	1.3			15.7				12.1	
Total	100.1		419.3	100.0			45.5(75.5)		
Per Gram			4.2				.45(.76)		10.7(18.1)
Calcium %		.09							
Phosphorous %		.12							
Gross Energy		1617.6							

*Starch values determined by direct, starch-specific analysis.

**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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 61. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

EQUISETUM ARVENSE - 100%.

Item: *Equisetum arvense*

Importance Value Percent: .51

Species: Same - sterile shoots - 100%

Economy: Lake

Condition: Succulent

Rank: 10

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	15.0	5.6	84.0	10.3	5.6	57.7	26.3	0	31.3
Ether Extract	3.7	9.3	34.4	2.6	9.3	24.2	10.2	0	29.6
Fiber	17.5			21.6				1.2	
Nitrogen-free Extract	40.6	4.3	174.6	44.1	4.3	Unknown	Unknown	1.1*	Unknown
Ash	<u>23.3</u>			<u>20.5</u>				0	
Total	100.1		293.0	99.1			36.5		
Per Gram			2.9				.37		12.8

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 62. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
PINUS ALBICAULIS NUTS - 100%, SAMPLE #1.

Item: *Pinus albicaulis*

Importance Value Percent: .48

Species: Same - nuts - 100%

Economy: Mountain

Condition: Mature

Rank: 11

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	11.9	5.6	66.6	5.8	5.6	32.5	34.1	0	51.2
Ether Extract	21.8	9.3	202.8	8.2	9.3	76.3	126.5	0	62.4
Fiber	36.9			54.8				1.5	
Nitrogen-free Extract	27.2	4.3	116.9	25.6	4.3	Unknown (110.1)*	Unknown (6.8)		Unknown (5.8)
Ash	2.2			5.5				2.5	
Total	100.0		386.3	99.9			160.6(167.4)		
Per Gram			3.9				1.6(1.7)		41.0(43.5)
Calcium %		.014							
Phosphorous %		.33							

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 63. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:

PINUS ALBICAULIS NUTS - 100%, SAMPLE #2.

Item: *Pinus albicaulis*

Importance Value Percent: .48

Species: Same - nuts - 100%

Economy: Mountain

Condition: Mature

Rank: 11

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	11.9	5.6	66.6	6.9	5.6	38.6	28.0	0	42.0
Ether Extract	21.8	9.3	202.8	1.0	9.3	9.3	193.5	0	95.4
Fiber	36.9			63.7				1.7	
Nitrogen-free Extract	27.2	4.3	116.9	23.9	4.3	Unknown (102.8)*	Unknown (14.1)	0	Unknown (12.1)
Ash	2.2			4.5				2.0	
Total	100.0		386.3	100.0			221.5(235.6)		
Per Gram			3.9				2.2(2.4)		56.4(61.5)
Calcium %		.014			.28			20.0	
Phosphorous %		.33			.19			0	

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 64. GRIZZLY BEAR FOOD QUALITY AND DIGESTIBILITY AS INDICATED BY CHEMICAL ANALYSIS:
RUSSULA SP. - 100%.

Item: *Russula* sp.
 Importance Value Percent: .03
 Species: Same - 100%
 Economy: Valley/Plateau
 Condition: Mature
 Rank: 16

	Whole Food Material			Corresponding Scat Material					
	Proxi- mate Con- tent %	Caloric Values	Gross Kcals	Proxi- mate Con- tent %	Caloric Values	Undi- gested Kcals	Apparent Digested Kcals	Concen- tration Factor	Minimum Apparent Digesti- bility %
Protein	23.3	5.6	130.5	7.8	5.6	43.7	86.8	0	66.5
Ether Extract	2.8	9.3	26.0	1.5	9.3	13.95	12.1	0	46.5
Fiber	12.1			29.0				2.4	
Nitrogen-free Extract	53.7	4.3	230.9	46.4	4.3	Unknown (199.5)*	Unknown (31.4)	0	Unknown (13.6)
Ash	8.2			15.3				1.9	
Total	100.10		387.4	100.0			98.9(130.3)		
Per Gram			3.9				.98(1.3)		25.0(33.0)

*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 shown in this category and elsewhere in parentheses to show the result if the values are accepted.

TABLE 65. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS:
CIRCIUM FOLIOSUM - 100%.
 Item: *Circium foliosum*
 Importance Value Percent: 4.4
 Species: Same - 100%
 Economy: Valley/Plateau
 Condition: Pre-flowering, Succulent
 Rank: 3

	Whole Food Material		
	Proximate Content %	Caloric Values	Gross Kcals
Protein	9.0	5.6	50.4
Ether Extract	1.8	9.3	16.7
Fiber	24.1		
Nitrogen-free Extract	52.3	4.3	224.9
Ash	<u>12.8</u>		
Total	100.0		292.0
Per Gram			2.9
Calcium %		.73	
Phosphorous %		.12	

TABLE 66. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS:
MICROTUS SP. - 100%.

Item: Rodentia
 Importance Value Percent: 1.3
 Species: *Microtus ochrogaster* - 100%
 Economy: Valley/Plateau
 Condition: Mature
 Rank: 7

	Whole Food Material		
	Proximate Content %	Caloric Values	Gross Kcals
Protein	69.8	5.6	390.9
Ether Extract	8.7	9.3	80.9
Fiber	2.2		
Nitrogen-free Extract	3.7	4.3	15.9
Ash	<u>15.5</u>		
Total	99.9		487.7
Per gram			4.9
Calcium %		3.91	
Phosphorous %		2.45	

TABLE 67. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS:
VACCINIUM SCOPARIUM BERRIES - 100%.

Item: *Vaccinium scoparium*
 Importance Value Percent: .37
 Species: Same - berries - 100%
 Economy: Valley/Plateau
 Condition: Ripe berries
 Rank: 12

	Whole Food Material		
	Proximate Content %	Caloric Values	Gross Kcals
Protein	9.7	5.6	54.3
Ether Extract	6.1	9.3	56.7
Fiber	13.9		
Nitrogen-free Extract	67.8	4.3	291.5
Ash	2.6		
Total	100.1		402.5
Per Gram			4.0
Calcium %		.22	
Phosphorous %		.18	

TABLE 68. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS:
HERACLEUM LANATUM - 100%, SAMPLE #1.

Item: *Heracleum lanatum*

Importance Value Percent: .14

Species: Same - 100%

Economy: Valley/Plateau

Condition: Pre-flowering, Succulent

Rank: 14

	Whole Food Material		
	Proximate Content %	Caloric Values	Gross Kcals
Protein	7.3	5.6	40.9
Ether Extract	2.2	9.3	20.5
Fiber	33.0		
Nitrogen-free Extract	44.5	4.3	191.4
Ash	13.4		
Total	100.4		252.8
Per Gram			2.5
Calcium %		1.09	
Phosphorous %		.31	
Gross Energy		1614.6	

TABLE 69. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS:

HERACLEUM LANATUM - 100%, SAMPLE #2.

Item: *Heracleum lanatum*

Importance Value Percent: .14

Species: Same - 100%

Economy: Valley/Plateau

Condition: Post-flowering, Succulent

Rank: 14

	Whole Food Material		
	Proximate Content %	Caloric Values	Gross Kcals
Protein	4.1	5.6	23.0
Ether Extract	1.5	9.3	14.0
Fiber	43.0		
Nitrogen-free Extract	43.5	4.3	187.1
Ash	7.9		
Total	100.0		224.1
Per Gram			
Calcium %		.49	
Phosphorous %		.26	
Gross Energy		1788.8	

TABLE 70. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS:

POLYGONUM BISTORTOIDES ROOTS - 100%.

Item: *Polygonum bistortoides*

Importance Value Percent: .07

Species: Same - roots - 100%

Economy: Mountain

Condition: Flowering, Succulent

Rank: 15

	Whole Food Material		
	Proximate Content %	Caloric Values	Gross Kcals
Protein	11.0	5.6	61.6
Ether Extract	1.2	9.3	11.2
Fiber	9.4		
Nitrogen-free Extract	71.4	4.3	307.0
Ash	<u>7.1</u>		
Total	100.1		379.8
Per Gram			3.8
Calcium %		1.19	
Phosphorous %		.22	
Gross Energy		1678.2	

TABLE 71. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS:

FRAGARIA VIRGINIANA FRUITS - 100%.

Item: *Fragaria virginiana*

Importance Value Percent: .02

Species: Same - fruits - 100%

Economy: Valley/Plateau

Condition: Ripe fruits

Rank: 17

	Whole Food Material		
	Proximate Content %	Caloric Values	Gross Kcals
Protein	9.8	5.6	54.9
Ether Extract	7.5	9.3	69.8
Fiber	13.7		
Nitrogen-free Extract	63.6	4.3	237.5
Ash	5.3		
Total	99.9		398.2
Per Gram			4.0
Calcium %		.33	
Phosphorous %		.33	

TABLE 72. GRIZZLY BEAR FOOD QUALITY AS INDICATED BY CHEMICAL ANALYSIS:

RIBES SETOSUM BERRIES - 100%.

Item: *Ribes setosum*

Importance Value Percent: .003

Species: Same - berries - 100%

Economy: Mountain

Condition: Ripe berries

Rank: 23

	Whole Food Material		
	Proximate Content %	Caloric Values	Gross Kcals
Protein	7.2	5.6	40.3
Ether Extract	5.2	9.3	48.4
Fiber	9.7		
Nitrogen-free Extract	66.7	4.3	286.8
Ash	<u>11.2</u>		
Total	100.0		375.5
Per Gram			3.8
Calcium %		.36	
Phosphorous %		.29	

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