

USE OF UNGULATES BY YELLOWSTONE GRIZZLY BEARS

Ursus arctos

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Abstract

Previous results of fecal analysis from the Yellowstone area and the known abilities of grizzly bears *Ursus arctos* to acquire and digest tissue from vertebrates suggested that grizzlies in this ecosystem obtained substantial energy from ungulates. This issue was addressed using observations from radio-marked grizzly bears, 1977–1992. Ungulates potentially contributed the majority of energy required for activity during the non-denning season for both adult female and male grizzlies. Most of this energy (95%) was estimated to come from the largest-bodied ungulate species (elk *Cervus elaphus*, bison *Bison bison*, and moose *Alces alces*), with greatest proportional contributions by scavenged adult male bison (16%), scavenged calf and yearling elk (10%) and adult female elk that were killed (8%) or scavenged (8%). Grizzlies acquired 30% of total edibles from ungulates by predation, of which 13% (or 4% of the total) came from predation on elk calves. Most scavenging occurred during the spring and was associated with the abundance and relative availability of different types of carrion. Predation and scavenging did not appear to be compensatory. Rather, total consumption of ungulates varied inversely with consumption of whitebark pine *Pinus albicaulis* seeds. The relative frequency of predation to scavenging increased with ungulate density. Contrary to previous suppositions, neither total ungulate use nor frequency of predation increased during the study, despite large increases in some ungulate populations. As expected by the identified trade-offs, Yellowstone grizzlies seemed to prey selectively upon moose, probably because of their solitary habits and forested surroundings, but otherwise favored vulnerable smaller-bodied ungulates such as elk calves. No predation on adult bison was observed. © 1997 Elsevier Science Ltd

Keywords: grizzly bear, elk, bison, moose, ungulates, predation, scavenging and Yellowstone.

INTRODUCTION

Grizzly bears *Ursus arctos* will typically eat meat whenever it is available. They are highly efficient at catching spawning salmonids and can be effective terrestrial sca-

vengers and predators. Several studies have found that moose in parts of Alaska and Canada were kept at low densities by heavy grizzly bear predation on calves (Boertje *et al.*, 1988; Larsen *et al.*, 1989; Ballard *et al.*, 1991; Gasaway *et al.*, 1992). Elsewhere, predation on ungulate calves has been associated with higher densities of black *Ursus americanus* and grizzly bears (Reynolds & Garner, 1987; Schwartz & Franzmann, 1991). Bear predation and scavenging are thus potentially important to understanding the dynamics of both ungulate and bear populations.

Most investigations of bear–ungulate relationships have dealt with a single ungulate species (typically moose *Alces alces*) and have focused on the ungulates rather than the bears. Although in many ways insightful, these studies have not revealed how total ungulate use or the frequency of predation by bears is likely to vary with ungulate species, the availability of alternate foods, or annual and geographic variation in ungulate numbers. All of these issues are relevant to anticipating the responses of bears to changes in their habitat, including the size and composition of ungulate populations — a concern especially where bear populations are small and isolated or heavily harvested.

Long-term studies of Yellowstone's threatened grizzly bear population provided an opportunity to address these broader issues, in addition to answering questions of immediate management concern. Prior analysis of grizzly bear feces from the Yellowstone area suggested that ungulates were an important food during the spring, and were also a more prominent part of the bear diet than in most parts of North America (Mattson *et al.*, 1991). Even so, consumption of meat was likely underestimated by fecal analysis because bears digest more of meat protein than any other nutrient (Hewitt, 1989; Pritchard & Robbins, 1989).

For these reasons, I hypothesized that ungulates were potentially a critical food for Yellowstone's grizzly bears, and that variation in ungulate populations affected bear behavior. Furthermore, because whitebark pine *Pinus albicaulis* seeds were known to be an important food (Mattson *et al.*, 1991, 1992), consumption of ungulates by bears was likely to be related to their consumption of pine seeds. There was also a common

perception that grizzly bear use of ungulates in the Yellowstone area had increased over time as a result of increasing ungulate populations. For example, French and French (1990) suggested that the frequency of elk calf predations had increased since 1984. I therefore questioned whether annual consumption of ungulates and relative frequency of elk calf predation were greater in 1984–1992 compared to 1977–1983, and whether use of ungulates was associated with use of whitebark pine seeds.

Several researchers have examined predation and meat consumption by different grizzly bear sex–age classes. Some studies found that larger lone bears, typically males, were more predatory (Boertje *et al.*, 1988; Gunther & Renkin, 1990), while other studies found no significant differences between adults of the two sexes (Ballard *et al.*, 1981; Reynolds & Garner, 1987). Cole (1972), alone, found that sub-adults and subordinate young bears were more effective predators. Boertje *et al.* (1988) also hypothesized that scavenging would be more common than predation where ungulate densities were higher. I, therefore, questioned whether consumption of ungulates and relative frequencies of predation were the same among different grizzly bear sex–age classes, and whether relative frequencies of scavenging compared to predation were the same or lower in areas where ungulate densities were higher.

I estimate parameters and describe relationships here that are relevant to these questions and hypotheses. The results are used to address questions with direct management implications, but also related to grizzly bear foraging behavior observed elsewhere.

STUDY AREA

The study area comprised the known range of Yellowstone's grizzly bear population. This 23 300 km² range included all of Yellowstone National Park and parts of six National Forests in Wyoming, Montana and Idaho in the United States of America. Conifer forest dominated >75% of the area, with non-forest vegetation common only at the highest and lowest elevations. The study area consisted of high elevation (>2100 m) plateaus surrounded by even higher elevation mountain ranges that extended beyond grizzly bear range or descended to lower elevation valleys and plains heavily used by humans for agriculture (Despain, 1990). Winters were cold and summers warm, with annual average temperatures near or slightly above 0°C. The majority of precipitation fell as snow, with winter accumulations reaching 20–260 cm before melting during March–June, depending upon elevation and latitude (Dirks & Martner, 1982).

Several ungulate species occupied the study area, including elk *Cervus elaphus*, bison *Bison bison*, moose, mule deer *Odocoileus hemionus*, whitetail deer *O. virginianus*, pronghorn *Antilocapra americana*, bighorn sheep *Ovis canadensis*, and mountain goats *Oreamnos*

americanus. Of these, elk and mule deer were the most abundant. During the past 20 years, populations of all ungulates except moose either remained stable or increased, with greatest increases exhibited by elk and bison in Yellowstone National Park since the end of herd reduction programs in the early 1970s (Mack *et al.*, 1990; Singer, 1990). More details concerning the study area can be found in Knight and Eberhardt (1985), Mattson *et al.* (1991), and Blanchard and Knight (1991).

METHODS

Radio-tagged grizzly bears were relocated from the air according to methods described by Knight and Eberhardt (1985) and Blanchard and Knight (1991). Of these aerial locations, a subsample was selected and visited to measure site parameters and determine the bears' activity (Mattson, 1997a). Subsampling was not random, but was representative of different bears and as close to complete representation of the aerial locations as possible. This approach was imposed by the large study area size, lack of road access, and administrative or legal restrictions on helicopter use.

All bear sign encountered while sampling bear locations was described according to a specified protocol (Mattson, 1997a). For ungulates, field crews noted the species, sex, age-class (based on tooth eruption and wear for elk, moose, and deer, and considering horn annuli for bison), marrow condition (according to Dalke, 1949 and Greer, 1969), and estimated time since death. During 1980–1981 jaws were collected from carcasses and the animals aged by analysis of cementum annuli. Bear use of carcasses was characterized as light, moderate, or heavy, and as predation or scavenging. Percent of edible biomass consumed by bears and, if possible, the number of bears involved were also estimated. Inferences concerning the numbers and identity of bears were based upon correspondence between information about the radio-marked bear and bear sign at carcass locations such as visual observations, track sizes, diggings, feces and beds. Predation was inferred from evidence of struggle, such as broken branches and gouges in dirt or bark, and the presence of internal hemorrhaging, broken vertebrae, and diagnostic claw marks on the carcass hide. The extent of carcass use by bears was inferred from the amount of bear sign as well as other diagnostic features of the carcass, such as hide manipulation, disarticulation, bone fracturing and relative locations of hair, rumen and skeletal remains (Mattson & Knight, 1992). Occasionally (<10%) inferences were based upon direct observation of bears using carcasses.

Given the great disparity in body size of different ungulate species, sexes and age-classes (~70×), and the comparable range in percent of that biomass consumed by bears (~20×), individual observations of carcass use potentially represented a >100-fold range in ingested biomass. Frequency of carcass use alone did not provide

Table 1. Estimates of edible dry weight biomass (in kg) for ungulate species and sex-age classes in the Yellowstone area. Where available, weights are given for summer-fall (Sm-Fll) and winter-spring (Wntr-Spr)

Ungulate type	Live weight		Skeletal weight ^c	Rumen weight ^d	Water weight ^e		Edible dry weight ^f	
	Sm-Fll ^a	Wntr-Spr ^b			Sm-Fll	Wntr-Spr	Sm-Fll	Wntr-Spr
Elk								
Calves (< 10 days)		18	1	0		14		3
Short-yearlings	136	108	10	9	74	60	43	29
Female, 2 years	180	144	14	14	96	78	55	37
Female, ≥3 years	233	156	19	16	123	82	76	40
Male, 3–7 years	249	167	20	18	131	90	80	39
Male, ≥8 years	292	196	24	23	152	104	93	45
Bison								
Calves (at birth)		23	1	0		14		8
Short-yearlings	158		12	16		85		44
Yearlings	271		22	35		142		73
Female, ≥5 years	440		38	62		223		118
Male, 5–9 years	676		60	99		334		182
Male, ≥10 years	784		71	116		384		212
Moose								
Calves (5 months)	180	144	14	14	96	78	55	37
Female, adult	385	258	32	32	197	135	123	58
Male, adult	446	299	38	39	226	155	143	67
Mule deer								
4 months		21	2	0		15		3
≥8 months		34	4	3		23		4

^aSummer-fall weights were taken from Blood *et al.* (1967), Anderson (1981), Houston (1982) Saether and Haagenrud (1982) and Berger and Peacock (1988).

^bWinter weights were inferred from Mitchell *et al.* (1976) and Houston (1982) — up to 36% weight loss over-winter in elk — and Anderson (1981) — 20–22% weight loss over-winter in mule deer.

^cSkeletal weight (*SW*) was estimated as a function of body weight (*BW*): $SW = 0.031BW^{1.123}$, and $SW = 0.061BW^{1.090}$ (Robbins, 1983), averaged, on summer-fall weights.

^dRumen weight (*RW*) was estimated as a function of body weight (*BW*) from data in Houston (1982), assuming 50% water weight: $RW = -8.56 + 0.160BW$, and $\ln RW = -4.54 - 1.59 \ln BW$ for $BW < 100$ kg.

^eWater weight (*WW*) was estimated as a function of body weight (*BW*): $WW = 0.921BW^{0.90}$, and $WW = 0.579BW^{0.98}$ (Robbins, 1983), averaged.

^fEdible dry weight was estimated as live weight – skeletal weight – rumen weight – water weight.

the information that was needed to estimate annual and seasonal variation in bear consumption of ungulates. Published estimates of ungulate body mass and proportions of water, skeleton and viscera were used to estimate the dry weight biomass available for consumption by bears, by ungulate type, on a seasonal basis, where possible (Table 1). Ingested meat was estimated by multiplying available biomass by the percent consumed by bears (Mills, 1990). Although these estimations were not accurate, errors in this approach were predictably an order of magnitude less than inaccuracies associated with ignoring ungulate body size and percent consumption. This method was a systematic means of incorporating information on body mass and bear activity into observations of carcass use, without having the opportunity to weigh ungulates prior to their deaths or periodically weigh them while being consumed. Even if possible, these measurements would have disturbed the bears and their potential prey and endangered field personnel.

Sampling intensity was not equal among years or months. Given that consumption of ungulates by bears, both total and of different ungulate types, also varied among years and months, the raw data were clearly biased with respect to some important estimations and

hypotheses. These biases were corrected by multiplying individual observations of carcass use by a weighting factor that was inversely related to month- and year-specific sample sizes. This factor was standardized to the month or year with the largest sample size (= 1). Thus, an observation of carcass use that occurred during a month or year with less than maximal sampling intensity was given more weight in annual or seasonal calculations of meat consumption, to correct for under-representation of the time period in the unadjusted sample.

Bear use of small ungulates and types of use, such as scavenging, characterized by smaller meal sizes are predictably underestimated by aerial relocations spaced at > 1 day intervals (Fuller & Keith, 1980), as in this study where time between relocations averaged 6 days. Carcasses used for longer periods of time or by greater numbers of bears were more likely to be detected. This bias was corrected by multiplying each observation by the inverse of mean bear-days of use for the associated type of carcass (Fuller & Keith, 1980). There were enough observations published ($n = 13$) or made during this study ($n = 3$) where duration of bear use and carcass type and consumption had been recorded to relate carcass size (X , as kg dry weight) to days of use (\bar{Y})

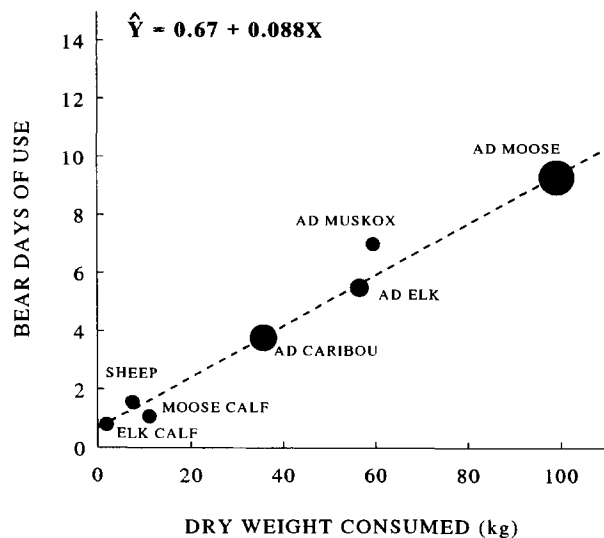


Fig. 1. The relationship between bear-days of use (\hat{Y}) and kg dry weight consumed from ungulates killed by brown or grizzly bears (X). Points corresponding to the mean for each ungulate type vary in size proportional to sample size of observed use (total $n = 16$). Edible dry weight was estimated by the same methods used in Table 1; for caribou based on Miller (1982). Observations are from Magoun (1979), Ballard *et al.* (1981), Griffel and Basile (1981), Murie (1981), Elgmork (1982), Schleyer (1983), Schleyer *et al.* (1984), Haroldson and Mattson (1985), Boertje *et al.* (1988), Gunther and Renkin (1990), French and French (1990) and Case and Stevenson (1991).

(Fig. 1). Each carcass type constituted an observation in this model ($n = 7$) weighted by sample size ($r^2 = 0.99$, d.f. = 1/5, $F = 468.8$, and $P < 0.001$).

Average annual frequency of ungulate use for individual bears of different sex-age classes was calculated, accounting for the effects of carcass size and seasonal sampling intensity. Frequency of use, by ungulate type and month, was multiplied by the inverse of estimated duration of use, in days, calculated using meat consumption per bear (rather than total). This number summed over ungulate types was divided by the number of days represented by the total sample of bear locations, and then multiplied by number of days in the month during which bears were not denning to estimate frequency of ungulate use. Total annual frequency was calculated by summing totals for months.

Total energy expenditures by an average adult Yellowstone grizzly bear and the percent of that expenditure potentially met by consumption of ungulate meat was calculated, with slight modifications, according to the methods of Schwartz and Franzmann (1991). Total energetic costs per bear (EC , in kJ day^{-1} , where $1 \text{ kJ} = 0.239 \text{ kcal}$), not including the costs of hibernation and female reproduction, were estimated as:

$$EC = AC(287BM^{0.712}).$$

The activity cost factor (AC) equaled 2.7 for males and 1.4 for females. These values were based on differences

in annual range size between the sexes and a summary of AC for larger mammals, ranging from 1.2 to 2.7, by Robbins (1983). Mean size of adult female annual ranges (281 km^2) was 32% that of adult males (874 km^2) (Blanchard & Knight, 1991). A high AC value was used for males given their large ranges compared to other terrestrial mega-vertebrates (Eisenberg, 1981). The relationship of basal metabolic rate to BM (average body mass = 123 kg for adult females and 184 kg for adult males) was developed for carnivores by McNab (1989).

Total energy derived from meat (EA , in kJ) during an average year was estimated as:

$$EA = 0.88(22.8MT),$$

where 0.88 = metabolizable energy as a proportion of gross energy (Pritchard & Robbins, 1989), 22.8 = kJ gross energy available from 1 g of meat, and MT = g of meat estimated to have been used by an average bear. $EA/(AD \times EC)$ gave the proportion of total active (i.e. non-denning) season activity costs covered by meat, where AD = the number of days between last and first radio-relocations at den sites (224 days for adult males and 188 days for adult females).

Estimated numbers of ungulates and proportional representation of habitat types in the study area were used to relate observed bear behavior to geographic variation in availability of ungulates and other important foods. Habitat type area was calculated from digital data for Yellowstone National Park (Despain, 1990), using the area of habitats able to support whitebark pine forests as an indicator of whitebark pine seed availability. Estimated sizes and compositions of ungulate populations were used to test whether observed bear use of species and sex-age classes was random and for calculating ungulate densities in different parts of the study area. Population estimates were taken from Houston (1968), Ritchie (1978), Singer (1990, 1991) and Mack *et al.* (1990) and sex-age class ratios from Meagher (1973), Houston (1982), Cole (1983), Singer (1991) and Pac and Frey (1991). Expected proportions of elk calves were based upon an average of pregnancy rates observed during a period of high population levels (1950–1962) and cow-calf ratios observed during the winter (Houston, 1982; Singer, 1991). Proportional availability of different ungulate types for the entire grizzly bear active season was derived from the sum of 2/7 weighted April–May values and 5/7 weighted June–October values. Results of spring ungulate carcass surveys on three winter ranges in Yellowstone National Park (Green, 1994) were used to calculate proportional availability of elk and bison carcasses during April–May. Mule deer and moose carcasses were not considered because surveys under sampled winter ranges of these two species.

Some analyses were stratified by season (April–May, June and July–October) to account for physiological changes in the bears and changes in availability of different carcass types. April–May corresponded to post-denning lethargy and the availability of winter-killed ungulates (Nelson *et al.*, 1983; Green, 1994). June coincided with peak estrus among Yellowstone's grizzlies (Craighead *et al.*, 1995), as well as peak elk calving (Johnson, 1951). July–October corresponded to elevated bear feeding typically associated with hyperphagia (Mattson *et al.*, 1991).

Statistical analysis of relationships depended upon the data structure and hypothesis. Log-likelihood (G) tests were used for goodness-of-fit and contingency table analysis, where hypotheses dealt with the independence of frequency distributions. Fisher's exact test was used where appropriate. The effects of several categorical factors and their interactions upon a categorical response were examined by modelling logits, using maximum-likelihood parameter estimation (Trexler & Travis, 1993). Because cell sample sizes were unequal, unbalanced analysis-of-variance (ANOVA) was used to address hypotheses regarding the equality of means or locations, employing parametric techniques where data were normal or could be normalized by transformations (ranks or natural log). Non-parametric techniques (Mann–Whitney (MW) and Kruskal–Wallis (KW) tests) were used in the remaining cases. The Tukey–Kramer procedure was used for multiple comparisons of parametric data (Day & Quinn, 1989); a non-parametric equivalent of the Tukey test for non-normal data (Zar, 1984); and a multiple comparisons procedure based upon angular transformations to compare proportions (Zar, 1984). Multiple comparisons were conducted only after a global test and at $\alpha = 0.05$.

Regression analysis was used to describe the relationships of: predation to species and body size; meat consumed by scavenging to carcass availability; probability of carcass use by > 1 bear to carcass mass; and relative frequency of predation to ungulate density. Transformations were used to normalize data or linearize relationships, weighted regression (by sample size) in cases where measurement of the dependent variable was estimated with varied confidence (Weisberg, 1985), and logistic regression where the dependent variable was categorical and the independent variables continuous (Trexler & Travis, 1993). Where relevant, the effects of ungulate species were examined by analysis-of-covariance (ANCOVA), controlling for the effects of carcass body mass.

Where the hypothesis that an observed was not different from an expected frequency distribution had been rejected, individual classes were identified where observed and expected proportions were not equal. Simultaneous Bonferroni confidence intervals were used to test equality of proportions for individual classes (Byers *et al.*, 1984), and where two estimated distributions were compared, confidence intervals varied with

sample sizes of both (Marcum & Loftsgaarden, 1980). Differences between observed and expected proportions were described by the Vanderploeg and Scavia electivity index (E) (Lechowicz, 1982), where:

$$E_i = (W_i - [1/n]) / (W_i + [1/n]), \quad W_i = (r_i/p_i) / \Sigma(r_i/p_i),$$

r_i = proportion of observations in the i th class, p_i = expected proportion in the i th class, and n = number of classes. This index potentially ranged from $+1$ to -1 , with positive values indicating selection for and negative values selection against a given class.

RESULTS

During 1977–1992, 1773 aerial relocations from 158 different radio-marked bears were visited and sampled (1–56 observations per bear, 49% female and 39% sub-adult), during which 211 instances of ungulate use were observed. An additional 48 observations of ungulate use by grizzlies were made during other related field work, not including ungulate carcass surveys (Green, 1994). Data were not collected systematically or at a comparable intensity from 1982 to 1985 because other study objectives were given priority. Observations of ungulate use were concentrated in Yellowstone Park, partly as a result of more intensive research in this area (Fig. 2).

Differences among ungulates

Total and monthly consumption

Most ungulate meat (53%) consumed by Yellowstone grizzly bears came from elk, followed by bison (24%), moose (18%), domestic livestock (cattle, sheep, and horses; 4%) and mule deer (1%). Very little of other ungulate species was eaten. The volumetric consumption of moose and bison was in excess ($20\times$ and $3\times$, respectively) of that expected by their relative numbers in grizzly bear range. Grizzlies procured 30% of all ungulate meat that they consumed by predation. Of the different species and sex–age classes, distinguishing carcasses that were scavenged from those obtained by predation, scavenged adult male bison, scavenged elk < 24 months old, and killed and scavenged adult female elk were the source of most meat eaten by grizzlies (Table 2). Elk calf predation provided 4% of total ungulate meat. Ungulates that died due to human intervention (i.e. road kills, domestic livestock, and bait) accounted for 8% of observations and 16% of total meat consumption.

Total consumption of ungulates (d.f. = 6/7, $F = 2.4$, $P = 0.033$) and the proportion contributed by predation varied among months (Fig. 3(a)). Consumption was highest in spring (April–May) and fall (September–October) and lowest in June and July. Average meat consumed per observation was also lowest during June,

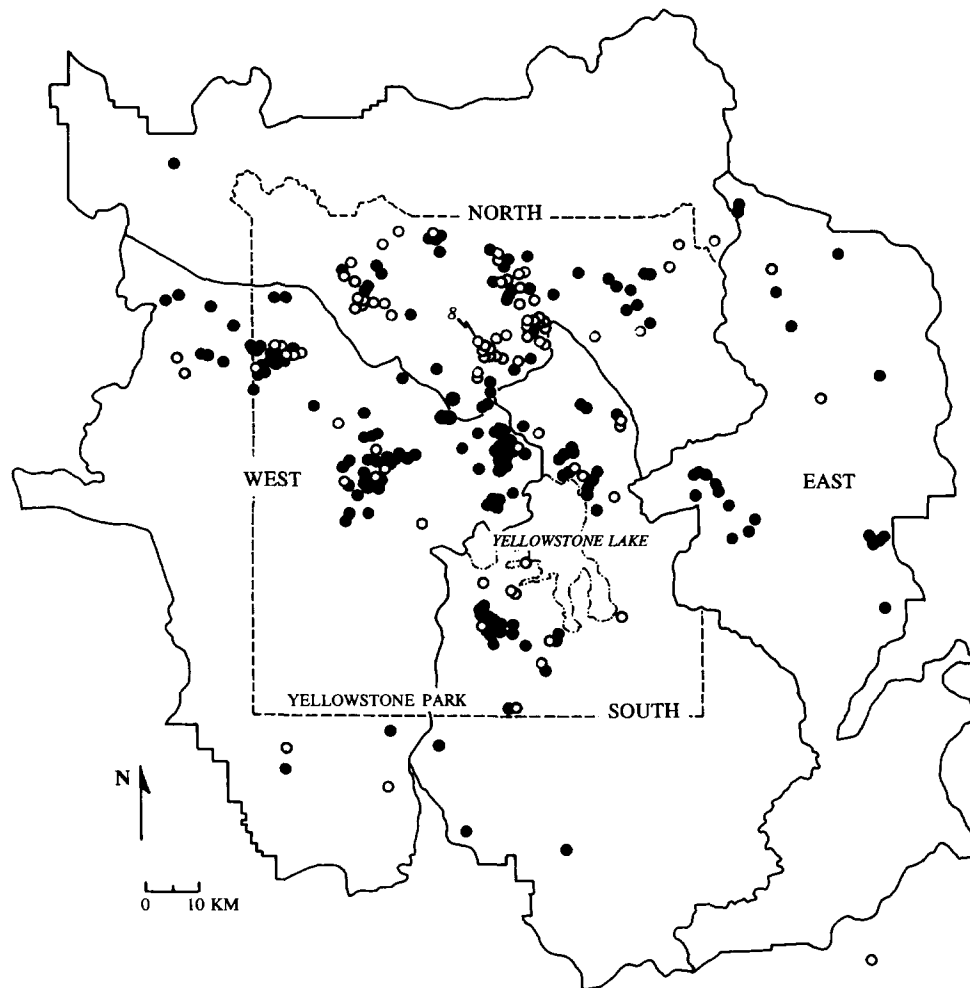


Fig. 2. Distribution of ungulates used by Yellowstone grizzly bears, 1977–1992. ○, predations; ●, scavenging. Yellowstone National Park and the four geo-vegetation provinces (North, East, South, and West) that were used to stratify this analysis are also delineated.

but highest in May, August and September (d.f. = 6/160, $F = 7.6$, $P < 0.001$) (Fig. 3(b)). Predation contributed relatively little (9%) of the total meat consumed during April–May, and contributed most to the bears' diet during October (58% of total ungulate meat) (Fig. 4). This was partly attributable to relatively more frequent predation on adult ungulates during July–October compared to the other two seasons (32% compared to 2% and 5% of the total observations for April–May and June; d.f. = 2, $G = 23.3$, $P < 0.001$). The relative frequency with which grizzlies used adult male ungulates by both scavenging and predation increased from 11% during April–June to 47% after July (d.f. = 1, $G_c = 29.1$, $P < 0.001$). Predation on elk calves was relatively most common during June, coincident with the calving season (71% compared to 24% and 3% during July–October and April–May; $G = 59.8$, $P < 0.001$). Relatively more meat was estimated to have been consumed during August–October from examination of carcass remains compared to analysis of feces (Mattson *et al.*, 1991). Predation on adult ungulates was most common and meal sizes the largest during this period (Fig. 3(a)).

Total biomass consumed per carcass varied considerably among ungulate species and sex–age classes, and depended upon whether the animal was carrion or prey (d.f. = 11/175, $F = 49.6$, $P < 0.001$) (Table 2). Largest amounts were consumed from scavenged male bison, and least from elk calf predations and mule deer, as expected primarily by differences in body mass. Among elk, however, bears consumed significantly more from prey than from scavenged animals of the same sex–age class, and differences were associated primarily with the type of bear use rather than body mass of the ungulate.

Selection of ungulate types

The frequency with which bears used different ungulate types varied from that expected by availability of live animals during April–May (d.f. = 7, $G = 63.2$, $P < 0.001$) and June–October ($G = 65.3$, $P < 0.001$), and year-round for predations ($G = 77.6$, $P < 0.001$). Adult female elk were used less than expected and elk calves more than expected by relative availability during all seasons (Table 3). Among bison, adults were not preyed upon by

Table 2. Relative biomass estimated to have been consumed from different ungulate types, for carrion vs prey, by Yellowstone grizzly bears, 1977–1992. The sample size (total and associated with sampling of radio-relocations), proportion of total biomass derived by predation, and average amount consumed per carcass, total and per bear, are also given for each ungulate type. Means followed by the same letters are not different at $\alpha=0.05$, only considering types with $n \geq 7$.

Ungulate type	Sample size		% Total biomass	% Total by predation	Mean total kg per carcass		Mean total kg per bear	
	Total	Reloc			\bar{X}	SE	\bar{X}	SE
Elk				43.0				
Calf (< 6 months) predation	39	29	3.8		5e	1.4	3bc	0.5
6–24 months, predation	6	6	2.6		40	4.2		
6–24 months, scavenging	25	17	10.4		15d	1.6	7bc	2.1
Adult female, predation	20	19	8.2		56bc	2.6	24abc	6.2
Adult female, scavenging	25	18	8.4		22d	3.6	15abc	4.2
Adult male, predation	13	10	6.2		54bc	6.0	30abc	10.0
Adult male, scavenging	14	10	6.5		16d	4.0	6bc	2.3
Unclass. adult, predation	13	11	0.8					
Unclass. adult, scavenging	3	3	4.4					
Unclass., scavenging	4	4	2.0					
Bison				4.0				
0–24 months, predation	2	1	0.9		45	—		
0–24 months, scavenging	6	4	1.8		24	10.6		
Adult female, scavenging	16	13	5.3		74abc	12.9	50ab	9.9
Adult male, scavenging	28	27	15.8		135ab	9.1	30abc	10.1
Moose				46.0				
0–24 months, predation	3	2	0.5		23	—		
0–24 months, scavenging	3	2	2.4		31	6.1		
Adult, predation	7	6	7.6		94abc	15.6	68ab	19.3
Adult, scavenging	11	9	7.1		67abc	11.9		
Mule deer	11	10	1.0	38.6	2e	0.7		
Domestic livestock	10	10	4.2	2.8				

bears, yearlings were underused during June–October, and adult females were underused in April–May. Although statistically significant only during spring, selection (E) for moose was consistently the highest of all ungulates examined.

During spring, availability was better reflected in numbers of winter-killed rather than live ungulates. When observed spring bear use was compared to that expected by carcasses on ungulate winter ranges (Green, 1994), use was not independent of availability (d.f. = 5, $G = 1.4$, $P = 0.923$); i.e. there was no apparent selection.

Other features of predation

Much of the edibles that Yellowstone's grizzlies consumed from moose (46%) and elk (43%) were obtained by predation, in contrast to meat obtained from bison (4% of the total for this species). Relative frequency of predation was correspondingly highest on adult moose and elk calves < 6 months old, and lowest on bison of all sex–age classes and elk > 6 months old (Table 2). Log-linear analysis of differences between ungulates that were prey and scavenged carcasses showed that predation was associated with marrow condition (d.f. = 1, Wald $\chi^2 = 25.6$, $P < 0.001$) and species (d.f. = 3, Wald $\chi^2 = 15.8$, $P = 0.001$), but not with season or sex–age cohort. Model fit was adequate (d.f. = 2, Wald $\chi^2 = 1.5$, $P = 0.468$), given that lower χ^2 values are associated with less difference between observed and

predicted frequencies (Knoke & Burke, 1980). Of ungulates used by grizzlies, elk and moose and carcasses with marrow fat $\geq 70\%$ (classes 1–3) were much more likely to be prey than bison or mule deer or carcasses that had pink or red gelatinous bone marrow (classes 4–8).

Results from this study were consistent with prior expectations that prey selection would vary with prey body mass (Vezina, 1985). Both electivity for prey (\hat{Y}_1 , rank-transformed) and the relative frequency of predation (\hat{Y}_2 , natural log-transformed) were negatively related to usable carcass biomass (X , in kg dry weight) ($P = 0.045$ and 0.026 , respectively), conditional upon the species (d.f. = 4/4, $F = 8.9$, $P = 0.028$, and d.f. = 4/5, $F = 6.4$, $P = 0.033$, respectively, for the entire model):

$$\hat{Y}_1 = 4.995 - 0.654X, \text{ and}$$

$$\hat{Y}_2 = 1.816 - 0.424X.$$

Model intercepts were an average for the four ungulate species considered — elk, bison, moose, and mule deer. Controlling for the effects of body mass, electivity for moose was not only > 0 , but was also greater than that for any other species. Relative frequency of predation was also related to species; and, controlling for mass, frequency was > 0 for moose and elk, and greater for moose than for bison.

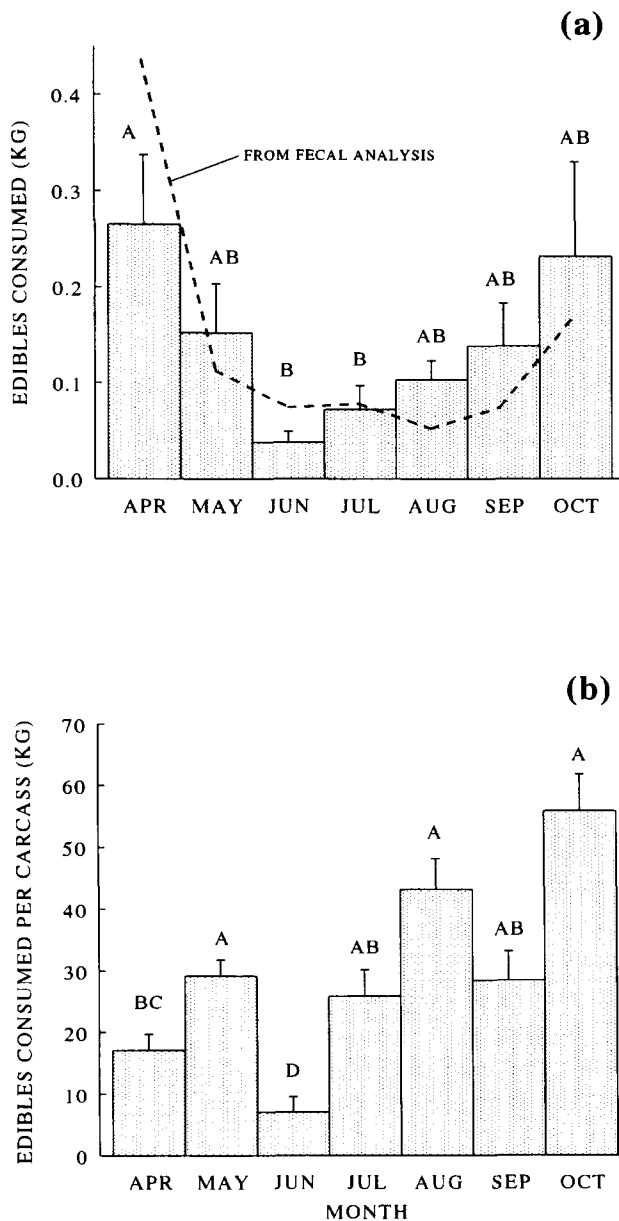


Fig. 3. Estimated (a) total volumetric consumption of ungulates; (b) mean total volume consumed by grizzlies from an ungulate carcass, by month, for Yellowstone grizzly bears, 1977–1992. The thick dashed line in (a) denotes relative volumes of ungulate remains (standardized to the entire active season) defecated by Yellowstone grizzly bears (Mattson *et al.*, 1991), estimated by the product of mean ungulate volume per feces and number of feces collected per sampled radio-telemetry location (Mattson *et al.*, 1991). Standard errors are shown and monthly means denoted by the same letters are not different.

Monthly frequencies of grizzly bear predation on elk calves from this study were independent of those reported by another study (Gunter & Renkin, 1990) from open areas of central Yellowstone Park (d.f. = 2, $G = 9.2$, $P = 0.010$). Calf predation was more frequent in July–August during this study (36% vs 4%), although both studies showed a June peak. In total, 69% of calf predations from this study occurred on forested sites,

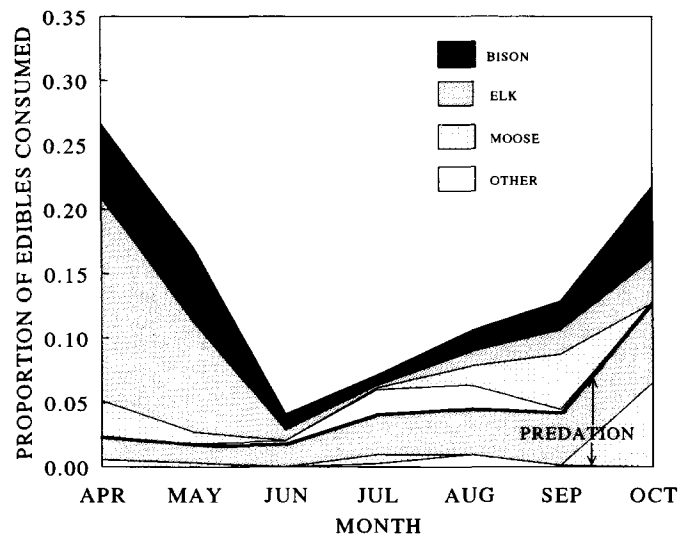


Fig. 4. Estimated proportions of total ungulates consumed by Yellowstone grizzlies, 1977–1992, obtained from elk, bison, moose and other ungulates, and by predation vs scavenging, by month. Individual monthly proportions summed across months = 1. The thick solid line delineates the proportion of ungulate meat that was obtained by predation.

with a slightly greater proportion in cover July–August compared to May–June (75% vs 67%).

Differences among years

Total consumption of ungulates varied among study years. Greatest consumption was observed during 1980 and 1989, and least during 1981, 1986, 1990 and 1991 (Fig. 5). Consumption of meat acquired by predation was annually more varied prior to 1982 than after 1985 (for equality of variances, d.f. = 4/6, $F = 149.6$, $P < 0.001$). There was no difference between the coefficients of variation for consumption of meat acquired by scavenging and meat acquired by predation for all years (d.f. = 11/11, $F = 1.27$, $P > 0.50$), although there tended to be greater variation in scavenging compared to predation during 1986–1992 (d.f. = 6/6, $F = 5.7$, $P = 0.052$). Meat consumed by scavenging was not annually correlated with meat consumed by predation ($n = 11$, $r = 0.210$, $P > 0.50$).

There was no difference in annual consumption of ungulate meat, total or by predation, between early (≤ 84) and late (≥ 85) years of the study (MW tests; $U = 36$ ($Z = 0.49$), $P = 0.626$, and $U = 42$ ($Z = 1.46$), $P = 0.144$, respectively). The relative frequency of total predation (40% vs 27%, for early and late years; $G_c = 2.54$, $P = 0.111$), and elk calf predation alone (23% vs 17%; $G_c = 0.65$, $P = 0.421$) also did not differ between study periods. Even so, average meat consumed per carcass was greater during the early compared to late period (29.2 kg vs 21.0 kg; d.f. = 1/151, $F = 7.9$, $P = 0.006$, for natural log-transformed values).

The relationship between frequency of scavenging during April–May and the number of winter-killed

Table 3. Electivity (*E*) for different ungulate types during spring (April–May) and summer–fall (June–October), and for predation year-long by Yellowstone grizzly bears, 1977–1992. Electivity is based upon comparing observed frequency of use with that expected by numbers of live animals in grizzly bear range. Electivity thus combines the effects of vulnerability (or relative availability as carrion) and selection

Ungulate type	Spring	Electivity summer–fall	Predation
Elk			
Calf < 6 months old		0.12** ^a	0.24**
6–24 months old	0.28**		0.13
Adult female	–0.58**	–0.82**	–0.80**
Adult male	–0.33	–0.41	–0.58
Bison			
0–24 months old	–0.08	–0.85	–0.76
Adult female	–0.67*	–0.67	–1.00
Adult male	–0.01	0.31	–1.00
Moose	0.45*	0.58	0.60
Mule deer	–0.13	–0.13	–0.30

^aUsing Bonferroni simultaneous confidence intervals.

** denotes significance at $\alpha = 0.05$.

* significance at $\alpha = 0.10$.

carcasses on winter ranges, 1986–1990, (d.f. = 1/2, $F = 58.5$, and $P = 0.016$) was more consistent with a type II than a type III functional response (Holling, 1959) in that the response appeared to be asymptotic and curvilinear (Fig. 6). The relationship was similar regardless of whether carcass counts from the Firehole or Northern winter ranges (Green, 1994) were used, and so was based on values averaged from both ranges. Although inconclusive because of a small sample size, these results indicated that use exceeded half-saturation ($0.5(dy/dx)$ at $\hat{Y}=0$) during six of the study years and three-quarters-saturation ($0.25(dy/dx)$ at $\hat{Y}=0$) during three years (in 1980, 1989 and 1992).

Annual frequency of ungulate use, June–October, was negatively related to the consumption of whitebark pine seeds during the same months. Annual consumption of whitebark pine seeds by grizzlies was either high or low because of an abrupt inflection in the relationship between bear use and seed crop size (Mattson & Reinhart, 1994). Years were accordingly classified as use or non-use based on a cut-point of 20% frequency of pine seeds in grizzly bear feces (Mattson *et al.*, 1992). If years were also classified by frequency of ungulate use during June–October, with a cut-point = 8, then high levels of

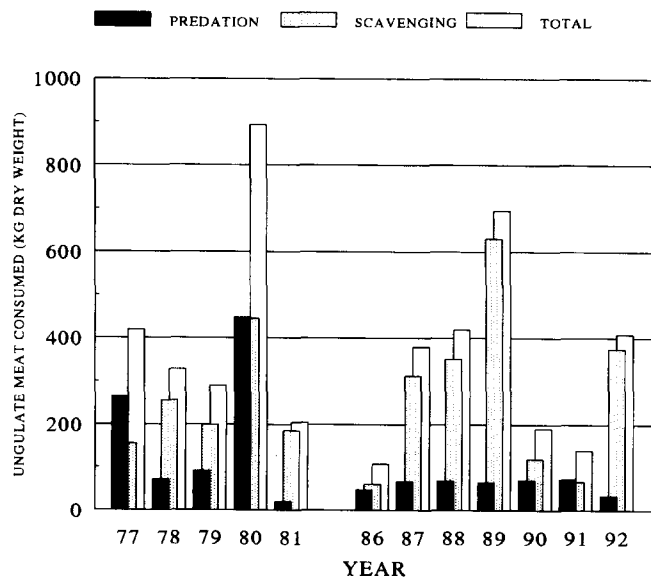


Fig. 5. Estimated annual volumetric consumption of ungulates by radio-marked Yellowstone grizzly bears, 1977–1992. Estimates were adjusted to compensate for variation in annual and monthly sampling intensities and for sampling biases attributable to ungulate body size. Totals attributable to predation and scavenging are also shown.

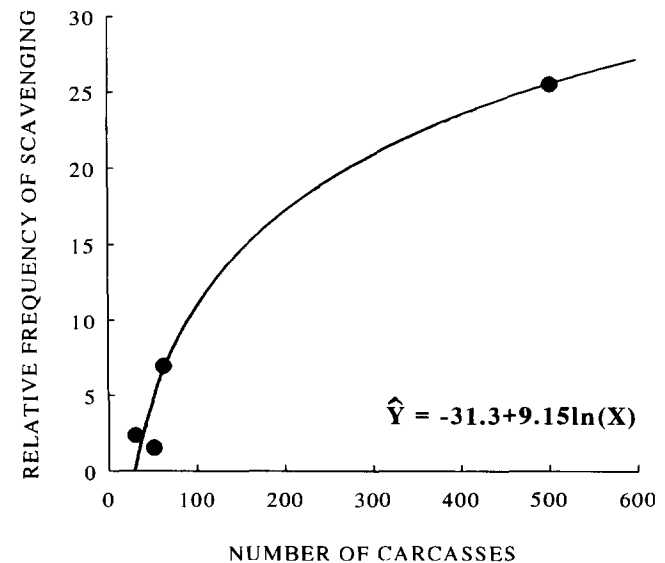


Fig. 6. The relationship between frequency of scavenging, April–May, and the number of ungulate carcasses on survey routes, averaged between two major ungulate winter ranges (Green, 1994), for Yellowstone grizzly bears, 1986–1990 ($n=4$ and $n=5$ for the Northern and Firehole winter ranges, respectively). The relationship assumes and is consistent with a type II functional response (Holling, 1959).

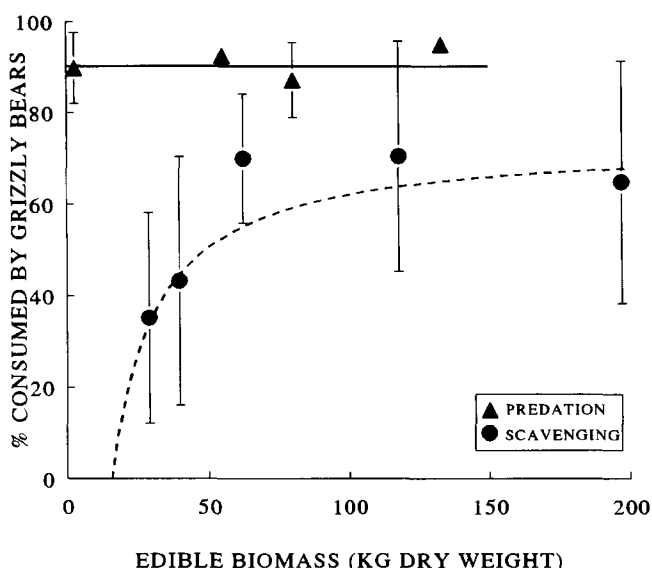


Fig. 7. The relationships between the percent of ungulate carcasses consumed by Yellowstone grizzly bears (bounded by 95% CIs), edible biomass of the ungulate (by methods in Table 1), and whether the ungulate was prey or carrion, for 1977–1992. Percentages were averaged by ungulate species and sex–age class.

ungulate and whitebark pine seed use were mutually exclusive. Similarly, frequency of ungulate use was $2.1\times$ greater during years when grizzlies did not use pine seeds compared to years when they did (11.0 vs 5.2 ; KW test, $U=33$ ($Z=2.4$), $P=0.016$).

Intra- and interspecific competition

When total meat consumed from a carcass was divided by the number of bears estimated to be present, this measure of meat/bear differed among ungulate types (d.f. = $8/156$, $F=5.2$, $P<0.001$, for natural log-transformed values). Individual bears consumed the most meat, on average, from adult moose prey and scavenged adult female bison, and the least meat from all classes of scavenged elk, as well as elk calves that were prey (Table 2). Meat/bear from adult female elk kills was not $>$ meat/bear from their scavenged counterparts, in contrast to a marked difference between these types of use for adult male elk.

The probability that only one bear used a carcass (\hat{Y}) was negatively related to total meat consumed (X , in kg dry weight) (d.f. = 1, Wald $\chi^2=25.5$, $P<0.001$):

$$\text{Logit}(\hat{Y}) = 2.78 - 0.023X.$$

Probability of involvement by >1 bear was 6% where meat consumption was ≤ 25 kg, 17% where consumption was 26–75 kg, and 52% where consumption exceeded 75 kg.

The percent of available biomass consumed by grizzlies varied by whether the ungulate was scavenged or their prey and, for scavenged carcasses, with body mass (Fig. 7). Percent consumption (\hat{Y}) was $1.7\times$ greater for prey compared to scavenged animals (90% vs 54%; MW test, $U=2322$ ($Z=6.87$), $P<0.001$), and increased as biomass potentially available from carrion (X) increased (weighted regression, d.f. = $1/3$, $F=35.5$, $P=0.010$):

$$\hat{Y} = 73.7 - 1159(1/X).$$

Because of this relationship, the difference between percent of available biomass consumed from prey and scavenged carcasses diminished with body mass of the ungulate, even though grizzlies still consumed a larger portion of large-bodied (>50 kg available biomass) prey compared to large-bodied carrion ($1.3\times$ more; MW test, $U=479$ ($Z=4.99$), $P<0.001$). This relationship also predicted that very little would be scavenged by grizzly bears from carcasses with ≤ 16 kg usable biomass (e.g. elk calves <6 months old and mule deer).

Differences among bears and areas

Differences among sex–age classes

Meat consumption varied substantially among grizzly bear sex–age classes (Tables 4 and 5). The frequency with which adult males used ungulates relative to all other activities was roughly $2.4\times$ that of adult females and subadult males and $7.2\times$ that of subadult females (d.f. = 3, $G=29.3$, $P<0.001$). However, there was no difference in the relative frequency of predation and scavenging among adult males, adult females, and sub-

Table 4. Estimated use of ungulates by different grizzly bear sex–age classes, Yellowstone area, 1977–1992; considering relative frequency of ungulate use at sampled radio-relocations, numbers of ungulates used and total ungulate biomass consumed per year, frequency of ungulate use per day during the non-denning period, and relative frequency of ungulate use that was by predation. Subadults were considered to be ≤ 5 years old. Proportions followed by the same letter in rows were not different at $\alpha=0.05$

Ungulate use	Grizzly bear sex–age class			
	Adult male	Adult female	Subadult male	Subadult female
Relative frequency	0.12a	0.05b	0.05b	0.02c
Number bear ⁻¹ year ⁻¹	13.8	5.5	4.8	1.1
Biomass (kg) bear ⁻¹ year ⁻¹	311	109	99	34
Number bear ⁻¹ active day ⁻¹	0.048	0.021	0.016	0.004
Relative frequency by predation	0.42a	0.25a	0.21a	0.22a

Table 5. Estimated annual per capita frequency with which adult Yellowstone grizzly bears used different ungulate types, for males and females, 1977–1992

Ungulate type	Grizzly bear adults	
	Male	Female
Elk		
Calf (<6 months) predation	2.8	0.8
6–24 months, predation	0.2	0.2
6–24 months, scavenging	2.8	1.1
Adult, predation	2.0	0.4
Adult, scavenging	3.2	2.0
Bison		
0–24 months, scavenging and predation	0.6	0.04
Adult, scavenging	0.8	0.3
Moose		
0–24 months, predation	0.3	<0.01
Adult, predation	0.5	<0.01
Adult, scavenging	<0.01	0.1
Mule deer	0.8	0.6
Other	0.4	<0.01

adults (d.f. = 2, $G = 3.8$, $P = 0.148$). Few observations of ungulate use by subadults precluded use of these bears in other analyses of differences among sex–age classes. Adult males used $\approx 2.5\times$ as many ungulates and consumed $\approx 2.9\times$ as much ungulate meat compared to adult females. There was also no difference in the variance of ungulate use (arcsin-transformed proportions) among individual males ($n = 6$) compared to individual females ($n = 20$) (d.f. = 5/19, $F = 1.02$, $P > 0.50$), using animals with ≥ 20 sampled locations and $> 50\%$ of the sample from their adult years.

Ungulates potentially contributed enough energy, on average, to cover $\sim 88\%$ of basic activity costs for adult male grizzlies during the non-denning period. For females, this figure was $\sim 75\%$, but without considering their energetic costs of reproduction and lactation. Assuming that activity costs used in these calculations were approximately 80% of total for adult males and 60% of total for adult females (Sizemore, 1980), energy from ungulate meat potentially covered $\sim 70\%$ and 56% of total energetic costs for the two respective sexes.

Differences among areas

Seasonal ungulate densities and the proportional area of high-value habitat complexes varied among broad geovegetation provinces of the study area (Fig. 2 and Table 6). Compared to other areas, the West contained proportionately the fewest sites able to support whitebark pine forests (the source of high-energy-content pine seeds) and the least mesic non-forest area where grizzlies frequently grazed and excavated roots (Mattson *et al.*, 1991; Mattson, 1997a,b). Densities of large ungulates (elk and bison) were substantially higher in the North year-round compared to anywhere else.

Bear use of ungulates, as a proportion of the bears' total activity (d.f. = 3, $G = 18.2$, $P < 0.001$), and the fre-

quency of predation relative to scavenging (Fisher's exact test, $n = 105$, $P < 0.001$), also varied among areas. Relative frequency of total ungulate use was greatest in the North and West while the proportion of that use attributable to predation was highest in the North and lowest in the East. Total ungulate use was most frequent either where densities of large ungulates were highest (North) or where availability of whitebark pine and mesic non-forest habitat was lowest (West). Relative frequency of predation (\hat{Y} , arcsin-transformed) was positively related to year-round densities of elk and bison (X , natural log-transformed, weighted for season duration) (d.f. = 1/2, $F = 23.5$, $P = 0.040$):

$$\hat{Y} = -24.9 + 12.8X.$$

DISCUSSION

The importance of ungulates to grizzly bears

Although the energy estimates presented here are necessarily ball-park approximations, they are consistent with the hypothesis that Yellowstone grizzly bears derived much of their energy from ungulates. Even if actual contributions were less, this difference would have to be quite large to support a different conclusion. The frequency of ungulate use by individual grizzlies corroborate the importance of ungulate meat. The 5.5–13.8 ungulates scavenged and killed by an average Yellowstone grizzly each year betoken a major dietary contribution when compared to the 8.5–16.6 ungulates killed on average by smaller-bodied, but strictly carnivorous, wolves *Canis lupus* (Keith, 1983).

This prominence of ungulates in the Yellowstone grizzly bear diet is plausible. The Yellowstone area supports some of the highest native ungulate densities in North America (especially compared to many wolf study areas (Fuller, 1989). Furthermore, when grizzly bear diets are estimated from uncorrected fecal analysis, there will be a very strong bias against meat use (Hewitt, 1989). Most prior assessments of ungulates in grizzly bear diets or the importance of ungulates to grizzly bear populations are, therefore, not reliable, as is the often-stated assertion that interior grizzly bears are almost wholly vegetarians. More useful assessments will use scat correction factors (Hewitt, 1989) or, as in this study, estimates based upon carcasses (Boertje *et al.*, 1988; Schwartz & Franzmann, 1991), with the proviso that sampling biases attributable to ungulate body size are corrected (Mills, 1991).

Variation in ungulate use

The frequency with which Yellowstone grizzly bears used ungulates varied considerably among months, years, and parts of the study area. This result was consistent with the varied food habits of Yellowstone's grizzlies (Mattson *et al.*, 1991). Vulnerability of ungulates to bears was likely affected by several factors,

Table 6. Relative frequency of ungulate use and proportion of that use by predation for grizzly bears, 1977–1992, by geo-vegetation province in the Yellowstone study area. Estimated ungulate densities, by species, and proportions of province in high-value habitat complexes are also given. No habitat data were available for the East. Proportions followed by the same letter in rows are not different at $\alpha = 0.05$

Province attributes	Geo-vegetation province			
	West	North	East	South
Bear use of ungulates				
Relative frequency	0.083a	0.072a	0.025b	0.038b
Proportion by predation	0.27bc	0.67a	0.12c	0.43b
Ungulate densities ($n/100 \text{ km}^2$)				
Elk	13 ^a /76 ^b	389/288	107/59	13/170
Bison	28/28	10/8	< 1	5/7
Mule deer	< 1/18	51/60	264/246	< 1/29
Habitat complexes (proportionate area) ^c				
Whitebark pine sites ^d	0.046	0.148	—	0.174
Mesic non-forest ^e	0.029	0.177	—	0.049
Total area (km^2)	6130	5880	5410	5640

^aWinter–spring estimate.

^bSummer–fall estimate.

^cProportions calculated from digital map data only for areas in Yellowstone National Park.

^d*Abies lasiocarpa/Vaccinium scoparium* — *Pinus albicaulis* habitat type phase, alone and in complex with other habitat types (Mattson & Reinhart, 1994).

^e*Festuca idahoensis* — *Agropyron caninum* and *Artemisia cana/F. idahoensis* habitat types, and *A. tridentata/F. idahoensis* — *Geranium viscosissimum* phase (Mueggler & Stewart, 1980).

given that grizzlies are versatile yet relatively ill-equipped for cursorial predation (Van Valkenburgh, 1985, 1989).

As anticipated, bear use of ungulates was related to whitebark pine seed use and densities of large-bodied ungulates. After May, when virtually all winter-kills had been scavenged (Green, 1994), grizzlies used ungulates the most during years when they used pine seeds the least. Ungulate use was also greater, aside from the effects of ungulate densities, in areas with fewer whitebark pine stands. For these reasons, it is likely that grizzly bear use of ungulates was in part compensatory to limited availability and use of whitebark pine seeds.

Total ungulate numbers also seemed to affect bear use, especially through availability of carrion on ungulate winter ranges. The relationship of April–May ungulate use to carcass numbers was consistent with a satiation or type II functional response, in that a continually smaller portion of added carcasses was apparently used by grizzlies. According to these results, demand by grizzly bears approached saturation (\leq one-quarter of dy/dx at carcass use frequency = 0) in only 3 of the 12 study years, and came closest to saturation during the mass ungulate die-off of 1989 that followed a severe drought and extensive wildfires during 1988 (Green, 1994). Frequency of ungulate use was similarly highest in the part of the study area with highest ungulate densities.

Yellowstone's grizzlies consumed the most ungulate meat during early and late months of the active season, in common with grizzlies in the eastern Rocky Mountains of the United States (Kendall, 1986; Aune & Kasworm, 1989) and brown bears throughout most of

the former Soviet Union (e.g. Ustinov, 1965; Novikov *et al.*, 1969; Zavatskii, 1978; Kaletskaya & Filinov, 1986). The April–May peak was associated with the highest frequency of scavenging and the greatest seasonal availability of carrion (Green, 1994). During the fall, bears consumed substantial amounts of both prey and carrion that were more equally comprised of elk, moose, and bison compared to other seasons. This season's use also coincided with the overlapping ruts of bison (July–August), elk (September), and moose (September–October), during which bulls were weakened, sometimes disoriented, and occasionally killed by each other (McHugh, 1958; Coady, 1982; Houston, 1982). The four-fold increase in the relative frequency with which grizzlies used adult male ungulates between April–July and August–October can thus be explained by greater vulnerability and mortality of bulls during the rut.

Even though use of ungulates by Yellowstone grizzlies was annually quite varied, there was no basis for concluding that either total ungulate use or frequency of predations on adults and calves was different between early (≤ 1984) and late (≥ 1985) years of the study. If anything, predation and total use were slightly greater earlier, possibly due to a lower frequency of good pine seed crops (Mattson *et al.*, 1992). Regardless, bear consumption of ungulates did not increase with herd sizes, possibly because this consumption was more directly related to availability of carrion and whitebark pine seeds than simply to numbers of live ungulates.

Use of different ungulate species and sex–age classes

Elk and bison accounted for > 75% of the ungulate biomass consumed by Yellowstone grizzly bears, while

bison and moose contributed to the Yellowstone grizzly bear diet far in excess of their relative numbers in grizzly bear range. This could partly be explained by the greater edible biomass on individuals of these two species, as well as the implicit likelihood that grizzlies would consume a larger portion of that which was available (Green, 1994). There was an additional tendency for Yellowstone's grizzlies to select moose. In contrast, despite the frequent use of mule deer and young elk calves by bears, they obtained relatively little meat from these two types of ungulates. Again, this could be partly explained by body mass. Both ungulates were among the smallest used by bears, and mule deer were often used as carrion, in competition with other scavengers.

Even though grizzlies selectively favored elk calves for predation, the contribution of these ungulates to the grizzly bear diet was inherently limited, not only by small body size, but also by marked declines in vulnerability after June and July (Gunther & Renkin, 1990). This does not mean that elk calf predation was infrequent during June, or that areas where this behavior occurred did not warrant management consideration, but rather that Yellowstone's grizzlies were not critically dependent upon this food source.

Features of predation

Approximately one-third of the ungulates used by Yellowstone grizzly bears were their prey, corresponding to ≈ 1.4 – 5.8 ungulates killed per adult bear per year, depending upon whether the bear was female or male. This rate was less than the 5.4 calves and 1.5 – 3.9 adults estimated to have been killed each year by grizzlies in east-central Alaska (Boertje *et al.*, 1988), but comparable to the 1.4 – 6.4 moose calves killed by black bears each year on the Kenai Peninsula of Alaska (Schwartz & Franzmann, 1991). Despite this relatively high frequency of predation, these results contrasted with Cole's (1972) observation that the majority of elk used by Yellowstone grizzlies were their prey. This may be due to differences in methods. Cole's study was based upon daylight observations in open areas, and was restricted to a relatively small portion of Yellowstone National Park.

Yellowstone grizzlies clearly benefited from predation. Most important, they were able to consume a larger portion of edible biomass at kills compared to scavenged carrion. In an area with some of the highest coyote *Canis latrans* densities in North America (Crabtree, 1993), competition with these more numerous scavengers for carrion was intense, especially for the more frequent smaller-bodied carcasses (Green, 1994). Grizzlies dominated other scavengers at carcasses (see Servheen & Knight, 1990), but many carcasses were consumed before any bear could find them (Green, 1994).

Yellowstone grizzlies apparently preyed more heavily upon smaller-bodied ungulates, and rarely killed the

largest ungulates in their range — adult bison. Strong selection for younger and smaller-bodied prey, especially within a species, has also been observed for the spotted hyena (Kruuk, 1972; Mills, 1990), and for wolves preying upon bison (Van Camp & Calef, 1987; Carbyn *et al.*, 1993), moose (Mech, 1970; Peterson *et al.*, 1984), and elk (Carbyn, 1983; Huggard, 1993). This pattern contrasts with the predictions of more simplistic optimal foraging models (see Stephens & Krebs, 1986) that anticipate predation upon the largest possible prey as a means of maximizing net energy return.

Given that grizzly bears are omnivores and well-suited to scavenging, their predatory activity likely depends upon availability of other feeding opportunities and the risks of injury. The benefits of predation relative to scavenging likely diminished for grizzly bears with increased ungulate body size, and plateaued for consumption of ungulates with > 50 kg of edible biomass. On the other hand, ungulates with < 16 kg of edibles appeared to be virtually unavailable to grizzlies if they died by causes other than bear predation (see also Green, 1994). There would thus be an incentive to prey upon small ungulates, especially if they were vulnerable, and little incentive to prey upon large ungulates, especially if there was substantial risk of injury — as would be likely when attacking the typically aggressive bison (McHugh, 1958; Carbyn & Trotter, 1987).

Prey selection by Yellowstone grizzlies was also apparently related to ungulate species, aside from effects of their body size. Moose were apparently most favored and bison and mule deer least favored for predation, consistent with positive selection for moose found by Novikov *et al.* (1969), Filinov (1980) and Boertje *et al.* (1988) in their study areas. These differences in selection could be explained by differences in the behavior of ungulate species, especially compared to other potential prey of the same general body size (Caro & Fitzgibbon, 1992). Moose were probably more vulnerable to bear predation than elk or bison because moose are more often solitary and more often inhabit forests where grizzlies can use the stalk and ambush techniques at which they seem to be more successful (e.g. Gunn & Miller, 1982; Schleyer, 1983; Gunther & Renkin, 1990). In contrast, female elk and bison tend to be more highly aggregated and more often in the open (McHugh, 1958; Houston, 1982). Because aggregation can be an effective predator defense (Caro & Fitzgibbon, 1992), it is not surprising that bison were preyed upon less often than comparable-sized moose. Mule deer were infrequent prey, plausibly because of their agility and speed, especially in contrast to elk calves, and their distribution in low-elevation areas less frequented by grizzlies (Mack *et al.*, 1990).

There was no indication that predation increased during years with fewer scavenging opportunities. However, the relative frequency of predation in different areas was positively related to ungulate density and the presumed frequency of encounter with potential prey. In

seeming contrast, predation was less frequent in Yellowstone compared to higher latitude study areas with lower ungulate densities. These results thus supported Boertje *et al.*'s (1988) hypothesis that predation was compensatory to either low prey densities or fewer scavenging opportunities at a scale that spanned study areas, but did not support their hypothesis within the Yellowstone study area itself. This discrepancy may be due to the effects of other scavengers. Although we lacked information on coyote abundance throughout the study area, we know that areas with the highest ungulate densities also contained extremely high coyote densities, i.e. the North (Crabtree, 1993). It may be that this factor had greater effects on grizzly bear predation than did ungulate densities alone, given that coyotes were major competitors for scavenging opportunities in the Yellowstone area (Green, 1994).

Intraspecific variation and competition

Individual grizzlies benefited if they could remain sole consumers of a carcass. This became increasingly unlikely as ungulate body size increased along with the time required to consume all odiferous edibles. Aside from this general tendency, individual bears were more likely to get their largest meals from adult moose and elk that were prey, and among bison, by scavenging adult females rather than the larger adult males.

Male grizzly bears used ungulates $> 2\times$ as frequently as females of the corresponding age class. However, given their larger average body mass and greater presumed activity costs, ungulate meat was estimated to cover only a slightly greater proportion of basic active-season energy needed by adult males compared to adult females, given that the energetic costs of reproduction were not included in calculations for females. When these costs were considered, there was a higher proportional contribution of meat to energy requirements of adult males compared to adult females, given that the greater activity ascribed to males probably accounted for most of their energetic costs of reproduction (Bunnell & Tait, 1981; Stirling & Derocher, 1990).

Different life strategies very likely maximize reproductive fitness of male and female grizzlies (Clutton-Brock & Harvey, 1983; Stirling & Derocher, 1990). Reproductive success of female bears seems to be contingent upon sufficient adipose reserves (Jonkel & Cowan, 1971; Rogers, 1976; Elowe & Dodge, 1989). By contrast, greater lean body mass logically gives males a competitive advantage in their relatively open promiscuous breeding system that sometimes involves violent confrontations with other males (Craighead *et al.*, 1995). Assuming that a high-protein diet promotes growth in lean body mass (see Bogin, 1988 and Speer, 1991 for other omnivores), greater consumption of high protein food by males would thus be expected, if for no other ultimate reason than the effects of increased fitness. On the other hand, more frequent use of ungulates may have simply resulted from larger male ranges and

the attendant increased probability of finding more carrion or vulnerable ungulates, combined with the ability of typically larger males to dominate concentrated high-quality foods (Egbert & Stokes, 1976; Craighead *et al.*, 1995).

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