

SPRING FEEDING ON UNGULATE CARCASSES BY GRIZZLY BEARS IN YELLOWSTONE NATIONAL PARK

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Abstract: We studied the spring use of ungulate carcasses by grizzly bears (*Ursus arctos horribilis*) on ungulate winter ranges in Yellowstone National Park. We observed carcasses and bear tracks on survey routes that were travelled biweekly during spring of 1985–90 in the Firehole-Gibbon winter range and spring of 1987–90 in the Northern winter range. The probability that grizzly bears used a carcass was positively related to elevation and was lower within 400 m of a road, or within 5 km of a major recreational development compared to elsewhere. Carcass use peaked in April, coincident with peak ungulate deaths. Grizzly bears also were more likely to use carcasses in the Firehole-Gibbon compared to Northern Range study area. We attributed the effects of study area and elevation to the fact that grizzly bears den and are first active in the spring at high elevations and to differences in densities of competing scavengers. Probability of grizzly bear use was strongly related to body mass of carcasses on the Northern Range where densities of coyotes (*Canis latrans*) and black bears (*U. americanus*) appeared to be much higher than in the Firehole-Gibbon study area. We suggest that additional restrictions on human activity in ungulate winter ranges or movement of carcasses to remote areas could increase grizzly bear use of carrion. Fewer competing scavengers and greater numbers of adult ungulates vulnerable to winter mortality could have the same effect.

J. WILDL. MANAGE. 61(4):1040–1055

Key words: bison, black bears, *Bos bison*, carcasses, *Cervus elaphus*, elk, grizzly bears, scavenging, *Ursus arctos*, winter mortality, Yellowstone National Park.

Grizzly bears in the Yellowstone region feed on ungulates more often than most brown and grizzly bears elsewhere in North America (Mattson et al. 1991). Ungulates may provide as much as one-half the energy required by Yellowstone's grizzly bears during the nondenning season (Mattson 1997). Much of this ungulate use is by scavenging during the spring (March–May), when elk (*Cervus elaphus*) and bison (*Bos bison*) energy reserves are at minimum (DelGiudice et al. 1991, 1994), and when mortality of these ungulates peaks (Meagher 1973, Houston 1982).

Most spring carrion in Yellowstone National Park occurs on ungulate winter ranges that are located at lower elevations, near human facilities such as roads and recreational developments (Craighead et al. 1973, Houston 1982). Previous Yellowstone studies of sign surveys (Reinhart and Mattson 1990) and radiotelemetry (Mattson et al. 1987) showed that grizzly bears under use areas influenced by high levels of human activity, including ungulate winter ranges near human facilities. Even so, it is possible that the diurnal radiotelemetry data used by Mattson et al. (1987) underrepresented griz-

zly bear use of areas near humans at night. Questions therefore remain regarding the severity of human effects on grizzly bear use of spring carrion.

Yellowstone's ungulate populations are dynamic. Their numbers, sex and age composition, and distribution during winter and early spring varied during the last 2 decades (Houston 1979, Meagher 1989, Mack and Singer 1992, Turner et al. 1994). The termination in 1968 of programs by the National Park to reduce bison and elk numbers resulted in population growth (Mack and Singer 1992), and compositions shifted towards older age classes (Houston 1979). Given the associated variation in availability of spring carrion (Houston 1978), both in numbers of carcasses and average carcass size, we anticipated that grizzly bears were affected.

The recent reintroduction of wolves (*Canis lupus*) into Yellowstone National Park likely will cause additional changes in Yellowstone's ungulate populations (Singer 1990a), with possible effects on grizzly bears (Servheen and Knight 1990). Wolves and bears likely will compete for carrion during the spring months (Servheen and

Knight 1990). Wolves may furthermore cause changes in herd compositions and in the inter-annual variability and total abundance of ungulate carcasses on winter ranges. These changes in ungulate herd and consequent carcass abundance are more likely to occur on smaller ranges in the Park interior (Singer 1990a) because these herds are smaller, non-migratory, and confined by deep snow (Craighead et al. 1973).

These expected effects of humans, wolves, and annual weather on carrion abundance led us to undertake a study of spring carrion use by bears. We tested whether bear consumption of carrion was selective with respect to species, sex, and age class of the carcass, and if selectivity varied by winter range and the abundance of carrion. We also tested whether selectivity was associated with cover, or human facilities. Because bear sign and ungulate carcasses exist at low densities, we focused our sampling on 2 winter ranges where carrion and grizzly bears were known to be concentrated during spring.

This study was funded by the U.S. National Park Service through the Interagency Grizzly Bear Study Team. R. R. Knight supervised the study team's research effort. We thank those who helped with fieldwork, including J. J. Jonkel, D. P. Reinhart, and especially J. Henry for his initial efforts and continued work in the Firehole-Gibbon study area. We appreciate reviews of this paper by E. D. Ables and P. Morgan.

STUDY AREA

Northern Range

The Northern Range study area paralleled the northern boundary of Yellowstone National Park and was bounded by Universal Transverse Mercator (UTM) coordinates 518–571 km east and 4,963–4,988 km north (Fig. 1). Elevations ranged from 1,585 to 2,475 m. This study area was located in the Yellowstone and Lamar river drainages, wholly within the Northern ungulate winter range described by Houston (1979). Large numbers of elk (ca. 20,000) and mule deer (*Odocoileus hemionus*; ca. 2,000) used this range during winter (Singer 1990b). Fewer bison (400–600), pronghorn (*Antilocapra americana*; 350–500), moose (*Alces alces*), and white-tailed deer (*O. virginianus*) were also present.

Climate here closely resembled that of the Great Plains (Despain 1987). Mean annual pre-

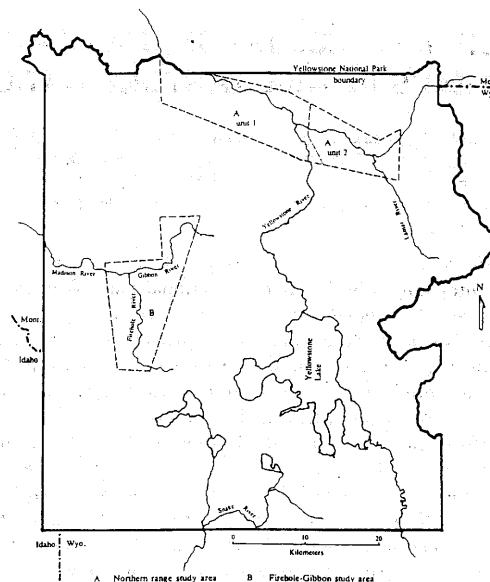


Fig. 1. Location of the Yellowstone National Park study areas—(A) Northern Range and (B) Firehole-Gibbon—where spring use of ungulate carcasses by bears was observed, 1985–90.

cipitation at Mammoth, Wyoming, was 40 cm and fell mostly during spring and early summer. Temperatures averaged 4.4 C for the year, and seasonal means varied from -4.8 C in January-March to 15 C in July-September (Dirks and Martner 1982).

Vegetation was a mix of grassland, shrub, and forest habitat types, with nonforest habitat types predominant (Despain 1990). Big sagebrush (*Artemisia tridentata*) and Idaho fescue (*Festuca idahoensis*) habitat types were common, while bluebunch wheatgrass (*Agropyron spicatum*) communities occurred on river sands and gravels. Tufted hairgrass (*Deschampsia cespitosa*) was abundant in seasonal wet areas, and sedges (*Carex* spp.) dominated marshes. Forests consisted mostly of Douglas-fir (*Pseudotsuga menziesii*), with lodgepole pine (*Pinus contorta*) abundant on drier sites and Engelmann spruce (*Picea engelmannii*) along streams and on seeps. Aspen (*Populus tremuloides*) communities occurred on some moist sites.

The Northern Range study area was divided into units 1 and 2 (Fig. 1), corresponding to lower and higher elevations. Unit 1 consisted of areas within the main Yellowstone River drainage. Unit 2 consisted of areas in the Lamar River drainage and on Specimen Ridge that ex-

tended eastward from the boundary between the 2 units at the confluence of the Yellowstone and Lamar rivers to the southern slopes of Mount Norris.

Firehole-Gibbon

The Firehole-Gibbon study area was bounded by UTM coordinates 507–526 km east and 4,921–4,955 km north and spanned a narrow elevational range of 2,164–2,316 m. This study area was restricted to the geothermally influenced winter ranges described by Meagher (1973) and Craighead et al. (1973), including upper parts of the Firehole drainage, the valley associated with the Gibbon River, and the Norris Junction geothermal basin. About 800 elk (Singer 1990b) and >200 bison (Meagher 1973) used this winter range.

The climate was colder and wetter than on the Northern Range (Despain 1987). Mean annual precipitation at West Yellowstone, the nearest long-term reporting station, was 57 cm and was distributed evenly throughout the year. The mean annual temperature was 1.6 C and averaged –8.5 C and 12.7 C for winter and summer months (Dirks and Martner 1982).

This study area was composed mostly of non-forest meadow and marsh habitats associated with geothermal activity (Despain 1990). Geothermally influenced vegetation reflected soil temperature, with barren ground and scattered moss on the warmest sites and moss, grass, and herb communities common under less extreme edaphic conditions (Sheppard 1971). Otherwise, graminoids dominated the majority of nonforested areas. Forested areas were dominated by lodgepole pine, with potential succession to subalpine fir (*Abies lasiocarpa*; Despain 1990).

METHODS

Field

Data were collected along nonlinear survey routes that were intended to maximize coverage of preselected portions of the winter ranges. Special landscape features that may have harbored an ungulate carcass, such as ravines, draws, benches, streambanks, mires, geothermal areas, forest edges, and small copses of timber in otherwise open terrain were searched. Areas of concentrated raven (*Corvus corax*) and/or coyote activity also were examined closely. Survey routes totaled 147.4 km in the Firehole-Gibbon and 306.5 km in the Northern Range study areas.

These routes were walked bimonthly, 1985–90 in the Firehole-Gibbon study area and 1987–90 in the Northern Range study area. Surveys started mid-March and ended mid-May except in the Firehole-Gibbon study area, where surveys started in mid-February during 1985–87 and ended during the first week of May in 1990.

Survey routes in the Firehole-Gibbon study area provided nearly complete coverage of the winter range. The Firehole-Gibbon range was relatively small (ca. 70 km²) and was well-defined by geothermal basins and drainages. In the Northern Range study area, however, survey routes were not as comprehensive and were delineated so as to maximize overlap between historical concentration of spring carcasses (Houston 1978) and spring locations of radiomarked grizzly bears (Mattson et al. 1987, Interagency Grizzly Bear Stud. Team [IGBST], unpubl. data). Survey routes on the Northern Range thus represented conditions previously associated with spring grizzly bear activity.

All discovered remains of ungulates that died during the spring or preceding winter were examined and noted. Species, sex and age of animal at time of death (methods described in Quimby and Gaab 1957, Robinette et al. 1957, Pac and Frey 1991), percent of carcass apparently consumed by bears, and total percent of carcass consumed by all scavengers were recorded. Percent of carcass consumption was relative to the edible biomass of a carcass, which did not include the skeleton, rumen, or hair. The estimate of bear consumption was determined by degree of carcass manipulation, number of bear scats with ungulate remains near the carcass, and amount of other bear sign nearby. Carcasses were reexamined during subsequent surveys and the percent of carcass consumed was again estimated. Where possible, date of first bear visitation was estimated from the age of bear sign near a carcass. This estimation was made only when first bear visitation occurred shortly before our discovery of the carcass.

Location (UTM), vegetation cover type (Despain 1990), distance to the nearest forest edge (m), distance to the nearest road (m), and distance to the nearest recreational development (km) were recorded for each carcass. In the Firehole-Gibbon study area, geothermal soil type was determined from maps produced by the Yellowstone National Park GIS Lab. Three geothermal soils were mapped: (1) silica/neutral hi chloride, (2) acid sulfate, and (3) travertine. A fourth "non-

geothermal" soil type was attributed to carcasses that were not located on these geothermal soils.

Bear tracks also were recorded. Bear tracks in a continuous line that were laid down by a single bear were considered a single track set. Location, bear species, track age, and distance to the nearest road were determined for each set. Distance to road of a particular track set was measured from the point where the tracks were closest to the road. When possible, the widths of pads from 4 tracks of each of the front and rear feet were measured (cm). For grizzly bears, tracks were categorized according to mean front pad widths for each track set: ≤ 11.0 cm, 11.1–13.5 cm, and > 13.5 cm. These size ranges roughly corresponded to small, medium, and large-sized bears. An analysis of front pad widths measured for radiomarked bears of known sex and age (IGBST data, see Blanchard 1987 for measurement methods) revealed that 80% of bears with front pads > 13.5 cm wide were adult (> 5 -yr-old) males and that 94% of bears with front pads < 11.1 cm were either cubs or subadults of either sex. Thus, these extreme categories were used to indicate rough levels of activity by adult males and young bears of either sex.

Analysis Methods

This analysis of the Firehole-Gibbon data differs from an initial analysis done by Mattson and Knight (1992) because it considers the effects of roads in the geyser basins that were closed to public but not administrative access, and because this analysis includes data from the Norris geyser basins and the Gibbon drainage. Roads used for analysis in this study were parts of the Grand Loop Road between Mammoth and Old Faithful and the barricaded Old Fountain Flats and Firehole Lake Roads.

We analyzed the availability and use of carcasses by bears during 4 seasonal periods: 17–31 March, 1–15 April, 16–30 April and 1–15 May. The 1989 data were analyzed separately because of anomalous conditions. Availability of carrion was far greater during 1989 compared to other years because of massive ungulate mortality following the drought and extensive wildfires ($> 568,000$ ha) of 1988 (Singer et al. 1989). For comparisons of carcasses used versus unused, we considered only ungulates that had died after 21 March in years other than 1989, and after 16 March in 1989, to be available to bears in the Northern Range study area. In the

Firehole-Gibbon study area, only ungulates that died after 14 March were considered available to bears. With the exception of certain carcasses mired in bogs, these were the earliest dates of death for ungulates that were later used by bears. Only carcasses with $> 5\%$ of their edible biomass consumed by bears were considered "used" by bears.

Although it could not be demonstrated, we know of no reason why carcasses used by bears would have a different probability of detection by field personnel than carcasses unused by bears. Thus for our analyses, we assumed carcasses used and unused were sampled with equal probability.

We described the relations between probability of carcass use by bears and individual independent variables by logistic regression analysis or by cross-tabulation. We did not have expectations regarding the exact form of these relations, and so used these univariate analyses to determine whether relations were linear, and for nonlinear relations, what the shape might be. We tested the fit of regression models and the independence of categories by the likelihood ratio statistic (G; Zar 1984, Demaris 1992: 4). Where we rejected independence, we identified categories where the probability of carcass use was significantly different than that expected by chance using simultaneous 95% Bonferroni confidence intervals (CI) that varied with the sample size of used and unused carcasses (Miller 1981). Point estimates of probability for continuous relations were calculated for purposes of illustration for equal percentiles, commensurate in number to the sample size of each variable.

We developed logit-based models (Demaris 1992) that described the probability of a carcass being used by bears as a simultaneous function of several independent variables: distance to the nearest road, distance to the nearest recreational development, distance to the nearest forest edge, seasonal time period, total number of available carcasses, elevation, edible biomass available from the carcass, and winter range identity. These models are equivalent to resource selection functions (Manly et al. 1993: 128). We developed a single unified model for grizzly bears as well as models specific to each study area. We also developed a model that differentiated carcasses used by black bears from those used by grizzly bears. Model fit was judged by the likelihood ratio statistic and pa-

parameter significance by the Wald χ^2 test (Wald 1943). Maximum likelihood estimates were used for all parameters (Demaris 1992:45). Probability of carcass use (\hat{P}) can be obtained by back-transforming the modeled logit (\hat{Y}): $\hat{P} = e^{\hat{Y}} / (1 + e^{\hat{Y}})$.

Each independent variable was structured according to insights gained from the univariate analyses. Distance to the nearest forest edge was configured so that carcasses located inside a forest stand were assigned negative values. Carcasses were classified by the amount of edible biomass available to scavengers to reduce the number of estimated parameters, and because we hypothesized that carcass type influenced bear use primarily through the availability of edible biomass. Edible biomass was assigned to each carcass type from tables in Mattson (1997).

We used the log-likelihood test (G ; Zar 1984: 52) to determine whether the number of bear tracks found on survey routes was independent of proportions expected by the length of survey routes at different distances from roads ($\alpha = 0.05$). Tracks and survey routes were grouped by even km distances, except in the Firehole-Gibbon study area, where a category ≤ 0.4 km was added (Mattson et al. 1987, Mattson and Knight 1992) because the larger sample size here allowed for greater resolution. If overall distribution of bear tracks differed significantly from random expectation, simultaneous confidence intervals (Byers et al. 1984) were calculated for each distance-to-road category to determine which contained a number of tracks significantly different from that expected by proportional survey effort.

We also used the log-likelihood ratio (G) to test whether the relative frequency of black bear tracks and grizzly bear tracks in the 3 size classes varied independently of the 2 Northern Range study units and the Firehole-Gibbon study area. Where independence was rejected, significant differences among areas were identified for each class with a multiple comparison procedure based on arcsine transformations (Zar 1984:401).

We developed nonlinear least-squares regression models to describe carcass depletion for 1989 and other years pooled. Carcasses were segregated into <1 year olds and adults for elk and ≤ 1 year olds, adult males, and adult females for bison. Separate models were developed for each of these classes. We did this be-

cause of the marked differences in size and weight of these species and age classes (Mattson 1997). Models were based on the Michaelis-Menten substrate saturation formula (Real 1977): $\hat{y} = k(x/[x+K_s])$, where k was maximum carcass depletion (asymptote = total percent consumed), K_s was the time (days) to 50% of maximum depletion, x was the number of days since the ungulate's death, and \hat{y} was the percent consumed.

Nonlinear least squares regression models also were developed to describe the relations between number of carcasses annually available and the number of these carcasses used by grizzly bears in each study area. These relations were based on the general formula for a logistic curve ($\hat{y} = i + [k/[1 + e^{a - bx}]]$), consistent with a Type III functional response to food availability (Real 1977). The NLIN procedure (SAS Inst. Inc. 1989) was used for model fitting.

RESULTS

Carcass Numbers and Distribution

The carcasses of 396 elk, 239 bison, and 1 mule deer were found in the Firehole-Gibbon study area, 1985–90. Most elk (69%) and bison (59%) were found in 1989 (Table 1). The carcasses of 741 elk, 18 bison, 15 mule deer, 14 pronghorn, 8 bighorn and 1 moose were found in the Northern Range study area, 1987–90. Most elk (76%), 6 bison, 4 mule deer, 12 pronghorn, and 3 bighorn were found in 1989. Peak availability of carcasses during the time that most bears were active (after 16 Mar) occurred during the 1–15 April time period on both ranges.

Carcasses in the Firehole-Gibbon study area were concentrated near roads and on geothermal soil types. During 1988 and 1989 there were more carcasses observed within 0.4 km of a road than expected by the relative distances traveled in this zone ($G = 13.1$, 2 df, $P = 0.002$, and $G = 46.0$, 3 df, $P < 0.001$, for 1988 and 1989). Although not statistically significant, almost half (47%) of the carcasses encountered on survey routes in 1987 were also within 0.4 km and a majority (60%) within 1 km of a road. A majority (73%) of the Firehole-Gibbon carcasses were located on geothermally-influenced soils. In 1989, more carcasses were located on acid sulfate soils ($G = 145.2$, 3 df, $P < 0.001$) than expected by the relative distances traveled across this soil type, while in 1988 more car-

Table 1. Number of elk and bison carcasses observed on survey routes during 1985–90 in the Firehole-Gibbon study area and during 1987–90 in the Northern Range study area, Yellowstone National Park. Carcasses are distinguished by whether they were found during 1989 or during other years (< >1989) and by the half-month time period during which the ungulate died.

Year, area, species	Time period					No date	Total
	≤16 Mar	17–31 Mar	1–15 Apr	16–30 Apr	1–15 May		
Firehole-Gibbon							
< >1989							
Elk	43	35	34	4	5	1	122
Bison	39	20	23	10	5	0	97
1989							
Elk	162	37	46	6	2	21	274
Bison	53	26	32	21	6	4	142
Northern range							
< >1989							
Elk	77	31	36	23	4	6	177
Bison	9	0	0	2	1	0	12
1989							
Elk	302	47	105	69	27	14	564
Bison	5	0	0	1	0	0	6

casses than expected were located on acid sulfate and travertine soils ($G = 12.7$, 2 df, $P = 0.002$). No relations with soil type was evident during 1987. No statistical tests were done for 1990 due to the small number of carcasses found on survey routes ($n = 7$).

Areas of geothermal influence were rare in the Northern Range study area and no comparisons between distributions of carcasses and geothermal soils were done. There was also no statistical evidence (all $P > 0.25$) that the dis-

tribution of carcasses varied with distance to roads in the Northern Range study area.

Carcass Depletion

Rates of carcass depletion varied with the species, sex, and age class of the ungulate and between 1989 and other years (Table 2). Except during 1989, elk carcasses were half-consumed, on average, within 1 day on the Northern Range and within 1 or 2 days in the Firehole-Gibbon area. Bison carcasses were half-consumed with-

Table 2. Parameter estimates (± 1 SE) for models of carcass depletion ($\hat{y} = k/x[x + K_d]$) for ungulate carcasses observed on survey routes in the Northern Range and Firehole-Gibbon study areas in Yellowstone National Park during 1989 and during all other years (< >1989) pooled. Carcasses were segregated by species, by age class, and by sex for adult bison.

Stratification	Year(s)	k ^a	K _d ^b	n ^c	r ²	F
Firehole-Gibbon						
Elk age class						
<1 yr old	< >1989	100 ± –	1.6 ± 0.63	60	0.95	1,092.9
Adult	< >1989	96 ± 9	1.4 ± 0.87	61	0.93	412.3
<1 yr old	1989	95 ± 8	7.2 ± 3.15	117	0.97	1,934.7
Adult	1989	95 ± 14	15.1 ± 7.00	192	0.89	762.5
Bison sex and age class						
Yearlings	< >1989	90 ± 17	2.0 ± 2.49	49	0.86	143.1
Cows	< >1989	100 ± –	5.3 ± 2.13	55	0.87	346.7
Bulls	< >1989	100 ± –	9.3 ± 5.63	30	0.81	119.8
Yearlings	1989	100 ± –	19.6 ± 5.61	84	0.79	314.9
Cows	1989	34 ± 33	6.2 ± 18.14	40	0.42	13.4
Bulls	1989	100 ± –	66.1 ± 30.10	33	0.69	70.1
Northern Range						
Elk age classes						
<1 yr old	< >1989	99 ± 1	0.1 ± 0.021	94	1.00	19,870.4
Adult	< >1989	98 ± 5	0.8 ± 0.35	94	0.96	1,162.5
<1 yr old	1989	79 ± 15	18.6 ± 11.41	293	0.71	357.1
Adult	1989	76 ± 18	57.1 ± 25.83	1,232	0.52	679.3

^ak = Asymptote or maximum amount of carcass depletion in percent (%); – denotes preselected values for k.

^bK_d = No. of days to 50% of maximum depletion.

^cn = No. of visits to carcasses.

Table 3. Number of grizzly and black bear track sets encountered on survey routes and per km of survey route traveled in the Firehole-Gibbon study area and in the Northern Range study area units 1 and 2 in Yellowstone National Park, 1987–90. The date on which sign of each species was first observed is also given.

	Year			
	1987	1988	1989	1990
Firehole-Gibbon study area				
Grizzly bear				
Date of first sign	28 Mar	24 Mar	16 Apr	25 Mar
No. of track sets (/km)	55 (0.151)	26 (0.102)	16 (0.045)	22 (0.056)
Black bear				
Date of first sign	12 Apr	none	23 Apr	24 Mar
No. of track sets (/km)	6 (0.016)	0 (0.000)	1 (0.003)	7 (0.018)
Northern Range study area				
Grizzly bear				
Date of first sign	23 Mar	23 Mar	29 Mar	25 Mar
No. of track sets (/km)—unit 1	6 (0.021)	5 (0.014)	3 (0.007)	2 (0.006)
No. of track sets (/km)—unit 2	15 (0.055)	12 (0.033)	13 (0.037)	10 (0.033)
Black bear				
Date of first sign	2 Apr	4 Apr	30 Mar	25 Mar
No. of track sets (/km)—unit 1	5 (0.018)	10 (0.028)	2 (0.004)	6 (0.017)
No. of track sets (/km)—unit 2	1 (0.004)	1 (0.003)	1 (0.003)	0 (0.000)

in about 2–10 days. Depletion of carcasses took longer during 1989 compared to all other years, except for adult cow bison. Time to half-depletion for this carcass type only increased from 5 to 6 days. However, maximum depletion of cow bison carcasses during 1989 was 34%, much less than the 100% depletion evident during other years. This lower asymptote for adult females and the increased number of days to 50% depletion of yearlings and bulls thus indicated substantially lower rates of per carcass consumption by scavengers during 1989, including bison. The r^2 values for the rate of depletion formulas decreased in 1989 for all carcass classes except those of elk <1 year old in the Firehole-Gibbon study area. This decrease, in concert with increased 95% CI, suggested that variation in the depletion of individual carcasses increased during 1989.

Distribution of Bear Tracks

Black bear and grizzly bear tracks varied in numbers and type between the Firehole-Gibbon study area and the 2 units of the Northern Range study area (Table 3). The number of grizzly bear tracks per kilometer of survey route in the Firehole-Gibbon area exceeded the number per kilometer in Northern Range units 1 and 2 by factors of 6.4–9.3 and 1.2–3.1, depending on the year. Grizzly bear tracks also were encountered more frequently in unit 2 compared to unit 1 of the Northern Range. The proportion of tracks attributable to black bears and to dif-

ferent size classes of grizzly bears differed between unit 1 and unit 2, of the Northern Range, and the Firehole-Gibbon study area ($G = 48.7$, 6 df, $P < 0.001$). Further, the proportions differed between unit 1 and unit 2 of the Northern Range ($G = 33.3$, 3 df, $P < 0.001$), and between unit 1 of the Northern Range and the Firehole-Gibbon study area ($G = 39.2$, 3 df, $P < 0.001$). These differences were not attributable to proportional differences in the sizes of grizzly bear tracks. Rather, they were due to the greater proportion of black bear tracks in Northern Range unit 1 compared to both unit 2 and the Firehole-Gibbon study area. Even though there were more grizzly bear tracks in the Firehole-Gibbon area, the sizes of tracks and the species that made them did not differ between the Firehole-Gibbon and unit 2 of the Northern Range ($G = 1.2$, 3 df, $P = 0.770$). Throughout the study, the date on which grizzly bear sign was first documented occurred between 22 and 29 March for both study areas, except in the Firehole-Gibbon in 1989 when first sign was documented on 16 April.

The number of grizzly bear track sets observed 1987–90 differed from numbers expected by the length of routes travelled at different distances from roads in both the Firehole-Gibbon ($G = 20.7$, 4 df, $P < 0.001$) and Northern Range ($G = 12.4$, 4 df, $P = 0.016$) study areas. Fewer grizzly bear tracks than expected were encountered ≤ 0.4 km from a road in the Firehole-Gibbon study area, while more than ex-

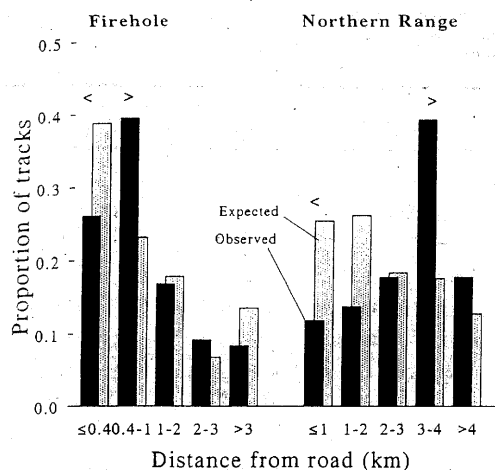


Fig. 2. The proportional distribution of grizzly bear track sets on Yellowstone National Park ungulate winter ranges compared to proportions expected by search effort (km of survey routes), categorized by km distance to the nearest road, for the Firehole-Gibbon and Northern Range study areas, 1987–90. Categories where the observed proportion of tracks was less than, or greater than, that expected by search effort ($\alpha = 0.05$) are denoted by '<' and '>'. Results for the Northern Range exclude survey routes in the Trout Lake area.

pected were encountered between 0.4 and 1.0 km (Fig. 2). In the Northern Range study area, fewer grizzly bear track sets than expected were encountered between 1 and 2 km of roads. Further examination of the Northern Range track data revealed that, of the track sets ≤ 1 km from highways, a majority (70%) were from the Trout Lake survey area. This area was anomalous because of security provided by topography and forest cover near the Mammoth-Cooke City highway. Without the Trout Lake data, there were significantly fewer grizzly track sets ≤ 1 km from highways in this study area ($G = 19.4$, 4 df, $P < 0.001$).

There was no evidence that the frequency of black bear track sets varied depending upon the distance to a road when data from 1987 through 1990 were pooled. The number of black bear tracks encountered ≤ 0.4 km from a road did not vary significantly from the number expected by search effort in the Firehole-Gibbon ($G = 0.4$, 1 df, $P = 0.567$) or the Northern Range ($G = 4.6$, 2 df, $P = 0.101$) study areas.

Carcass Use by Bears

Bears used 120 (8%) of all carcasses observed during this study. Of the 396 elk, 239 bison and 1 mule deer carcasses found in the Firehole-Gibbon study area, 41 elk and 43 bison were

used by grizzly bears. Black bears here did not use any carcass during 1989; although they used 2 elk and 4 bison during other years. Of the 741 elk, 18 bison, 15 mule deer, 14 pronghorn, 8 bighorn, and 1 moose carcasses found in the Northern Range study area, 14 elk were used by grizzly bears. Black bears used 13 elk, 2 bison, and 1 mule deer. Grizzly bears killed 6 (2 on the Northern Range and 4 in the Firehole-Gibbon study area) of the 55 elk that they used, and scavenged 4 other carcasses of ungulates mired in a bog on the Northern Range. Two of the bog carcasses were used in 1988, and 1 was used in each of 1989 and 1990.

The delay between time of ungulate death and first visitation of carcass by grizzlies was estimated on 10 (71%) of the Northern Range carcasses used by grizzlies and 30 (85%) of the Firehole-Gibbon carcasses used by grizzlies in the years 1986 through 1990. Of the 4 carcasses found mired in the bog on the Northern Range, average delay to first visitation by grizzlies was 48 days. All of the remaining 6 carcasses were encountered by grizzlies within the first 2 days. Of the Firehole-Gibbon carcasses with estimates of time to grizzly bear visitation, 15 (50%) were visited by day 3, 23 (77%) were visited by day 12 and all were visited by day 34.

Features of Grizzly Bear Use, Single Factors.—The probability that a grizzly bear had used a carcass varied with the species, sex, and age class of the dead ungulate ($G = 23.5$, 5 df, $P < 0.001$). A bear was more likely to use a bison compared to an elk carcass, and rarely used mule deer (Fig. 3). As implied by the previous results, probability of bear use was positively related to the edible biomass available from a carcass (Fig. 3). In the Northern Range this relation was described by: $\hat{Y} = -12.9 + 0.24X$, where \hat{Y} = logit of probability and X = edible biomass (kg; model fit $G = 3.9$, 5 df, $P = 0.564$; X parameter = 0, $\chi^2 = 6.0$, 1 df, $P = 0.014$). In the Firehole-Gibbon study area this relation was more complex (Fig. 4) and better described by a polynomial regression: $\hat{Y} = -2.41 + 0.03X - 0.00012X^2$ (model fit $G = 5.9$, 9 df, $P = 0.752$; X and X^2 parameters = 0, $\chi^2 = 6.0$, 1 df, $P = 0.014$ and $\chi^2 = 4.9$, 1 df, $P = 0.027$).

Probability of carcass use was also related to the nearness of human facilities in the Firehole-Gibbon study area, but not the Northern Range study area (Fig. 5). Probability of use of was less than expected ≤ 0.4 km from a road ($G = 16.1$,

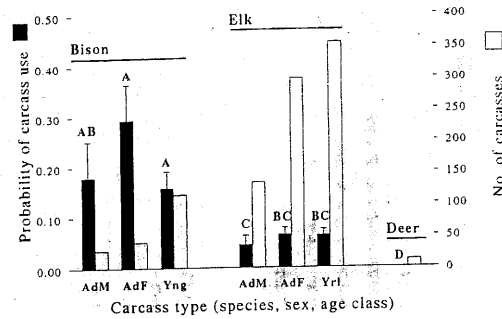


Fig. 3. The mean probability (± 1 SE) that carcasses of different ungulate species and sex and age classes had been used by grizzly bears in the Firehole-Gibbon (1985–90) and Northern Range (1987–90) study areas, combined. Total number of carcasses observed for each carcass type is also shown. Carcass types are adult male (AdM), adult female (AdF), animals ≤ 1 year old (Yng), and animals < 1 year old (Yrl). Mean probabilities that did not differ ($\alpha = 0.05$) are denoted by the same capital letter.

3 df, $P = 0.001$) and ≤ 5 km from a primary development ($G = 13.2$, 3 df, $P = 0.004$) in the Firehole-Gibbon study area. Results were not statistically significant on the Northern Range ($G = 3.7$, 3 df, $P = 0.299$, and $G = 0.5$, 1 df, $P = 0.470$, for road and development effects).

Distance to nearest forest edge affected probability of carcass use by grizzly bears in the Firehole-Gibbon ($G = 12.0$, 4 df, $P = 0.017$) but not the Northern Range ($G = 3.6$, 4 df, $P = 0.459$) study area (Fig. 6a). Probability of use declined as distance from forest cover increased

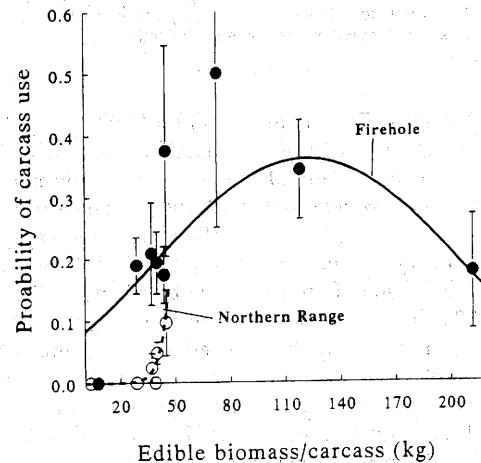


Fig. 4. The probability that a carcass had been used by grizzly bears on ungulate winter ranges in Yellowstone National Park as a function of available edible biomass (Mattson 1997), for the Firehole-Gibbon (1985–90) and Northern Range (1987–90) study areas. Each point represents the mean probability (± 1 SE) for a different carcass type.

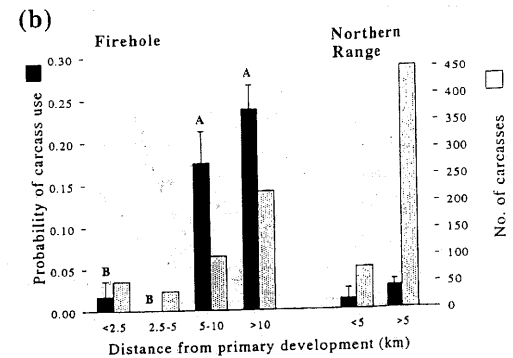
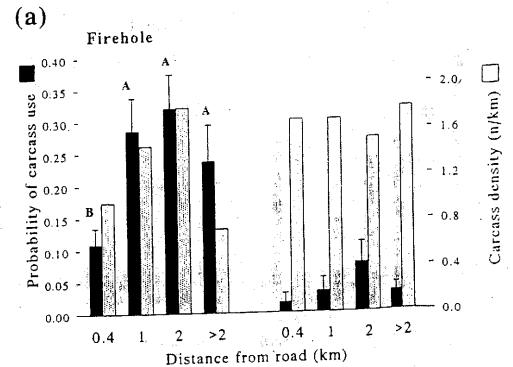


Fig. 5. The mean probability (± 1 SE) that a carcass had been used by grizzly bears on ungulate winter ranges in Yellowstone National Park as a function of distance to either (a) roads or (b) primary developments, for the Firehole-Gibbon (1985–90) and Northern Range (1987–90) study areas. Carcass density (n/km of survey route) is shown for each distance-to-road category, and total number of carcasses observed by distance to a development. Mean probabilities that did not differ ($\alpha = 0.05$), by study area, are denoted by the same capital letter.

to 175 m. Probability of use increased at distances > 175 m. In contrast to other univariate effects, elevation affected probability of carcass use by grizzly bears in the Northern Range but not the Firehole-Gibbon study area (Fig. 6b). The model describing the relation of probability of use (\hat{Y} , as a logit) to elevation (X , in m) was: $\hat{Y} = -13.4 + 0.0015X$ (model fit $G = 63.8$, 188 df, $P = 1.000$; X parameter = 0, $\chi^2 = 11.9$, 1 df, $P < 0.001$). Results for the Firehole-Gibbon study area were not significant ($G = 99.2$, 1 df, $P < 0.001$ for goodness-of-fit of the logistic regression model), but the pattern was consistent with that observed in the Northern Range study area.

Probability of use was related to variation in carcass abundance as a function of date-of-death and year. Date-of-death affected proba-

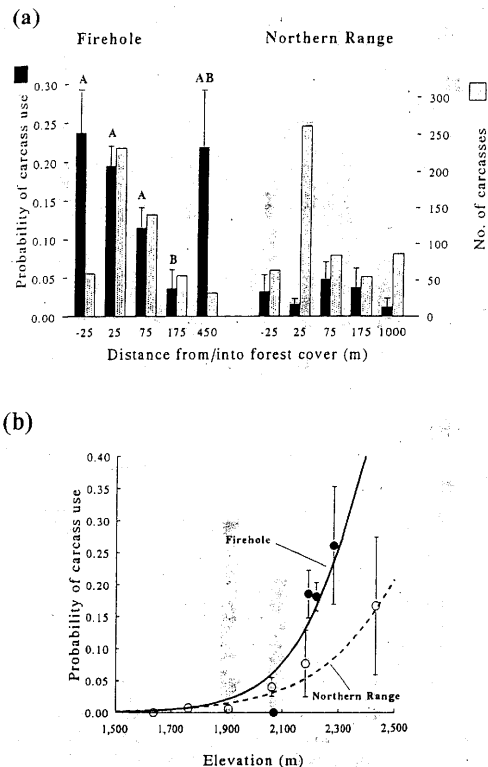


Fig. 6. The probability (± 1 SE) that a carcass had been used by grizzly bears on ungulate winter ranges in Yellowstone National Park as a function of (a) distance to the nearest forest edge (cover) and (b) elevation, for the Firehole-Gibbon (1985–90) and Northern Range (1987–90) study areas. Number of carcasses is shown for each distance-to-forest edge category. Mean probabilities that did not differ ($\alpha = 0.05$), by study area, are denoted by the same capital letter.

bility of grizzly bear use in the Firehole-Gibbon study area ($G = 24.2$, 4 df, $P < 0.001$), but not in the Northern Range study area ($G = 1.6$, 4 df, $P = 0.663$; Fig. 7a). Probability of use peaked during April in the Firehole-Gibbon area and generally corresponded to number of carcasses that had died during each biweekly period. Probability of use (\hat{Y}) was negatively associated with the number of carcasses (X , natural log transformed) annually available during the time that grizzly bears were active in both the Northern Range and Firehole-Gibbon study areas (for X parameter = 0, $\chi^2 = 7.5$, 1 df, $P = 0.006$, and $\chi^2 = 28.0$, 1 df, $P < 0.001$). Models for the 2 study areas were: $\hat{Y} = 0.61 - 0.84X$, and $\hat{Y} = 2.14 - 0.78X$ (Fig. 7b). Fit for each model was acceptable ($G = 4.0$, 2 df, $P = 0.138$, and $G = 5.4$, 4 df, $P = 0.250$).

Features of Grizzly Bear Use, Integrated

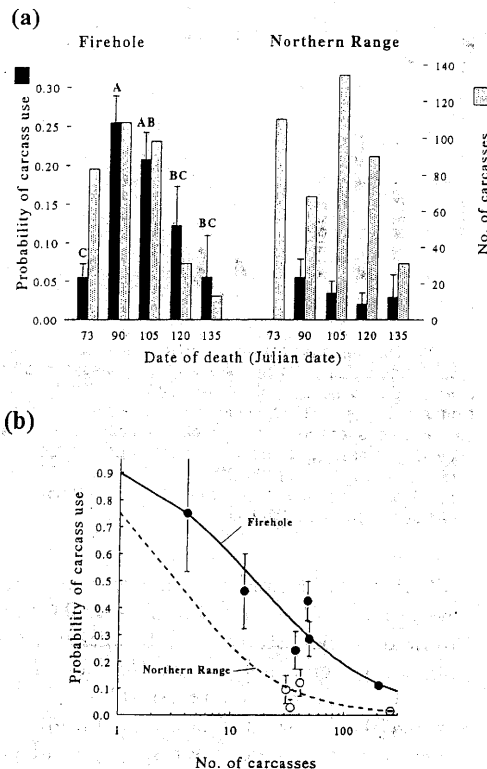


Fig. 7. The probability (± 1 SE) that a carcass had been used by grizzly bears on ungulate winter ranges in Yellowstone National Park as a function of (a) the date that the ungulate died and (b) the number of carcasses annually available, for the Firehole-Gibbon (1985–90) and Northern Range (1987–90) study areas. Number of carcasses observed by date-of-death category is given in (a) and points denoting the mean probability of carcass use for each study year in (b). Mean probabilities that did not differ ($\alpha = 0.05$) by date of death, by study area, are denoted by the same capital letter.

Models.—The model that described the relation of grizzly bear use to edible biomass, date-of-death, annual abundance of carcasses, elevation, distance to nearest forest edge, distance to the nearest road, distance to the nearest recreational development, and winter range identity provided a good fit to the observed use ($G = 291.4$, 802 df, $P = 1.000$). All coefficients, except for distance to nearest forest edge, were significant ($P < 0.05$; Table 4). The strongest relations were to carcass abundance (negative), date-of-death (negative for 14 Feb–14 Mar, and positive for 15 Mar–15 Apr), distance to the nearest primary recreational development (negative), and distance to the nearest road (negative). Probability of carcass use was higher in the Firehole-Gibbon study area compared to the Northern

Table 4. Parameter estimates (± 1 SE) for linear models that relate the probability of an ungulate carcass being used by grizzly bears (\hat{P}) as a logit $\hat{Y} = \ln(\hat{P}/(1 - \hat{P}))$ to independent variables related to site features, time of year, and carcass abundance. Models were developed for grizzly bears in each Yellowstone National Park study area (the Firehole-Gibbon for 1985-90, and the Northern Range for 1987-90) and for the 2 study areas combined. A model also was developed that describes the probability that a carcass used by bears was used by a grizzly rather than a black bear. Probabilities (\hat{P}) can be back-calculated from the modeled logit (\hat{Y}): $\hat{P} = e^{\hat{Y}}/(1 + e^{\hat{Y}})$. Probabilities (\hat{P}) that parameters = 0 were determined by the Wald χ^2 test.

Parameter	Both study areas				Model			
	Estimate ± 1 SE	P	Firehole-Gibbon	Northern Range	Estimate ± 1 SE	P	Estimate ± 1 SE	P
Intercept	-11.2 \pm 3.55	0.002	-3.2 \pm 1.36	-77.6 \pm 12.09	-6.54 \pm 17.531	0.000	-6.54 \pm 17.531	0.709
Carcass mass (kg)	0.041 \pm 0.0164	0.013	0.041 \pm 0.0169	2.61 \pm 0.214	0.038 \pm 0.0361	0.000	0.038 \pm 0.0361	0.492
Carcass mass squared (kg ²)	-0.00017 \pm 0.000076	0.029	-0.00016 \pm 0.000075	-0.030 \pm 0.0008	0.016 \pm 0.0042	0.000	0.016 \pm 0.0042	0.000
Elevation (m)	0.0048 \pm 0.00158	0.002		0.0058 \pm 0.00200		0.333 ^a		0.949 ^a
Distance to/into forest								
≤ 75 m	0.29 \pm 0.208	0.169	0.38 \pm 0.250	-0.39 \pm 0.403	0.049 \pm 0.764	0.333	0.049 \pm 0.764	0.949
> 75 m	-0.29 ^b		-0.38 ^b	0.39 ^b	-0.049 ^b		-0.049 ^b	
Carcass no. (ln(n))	-1.08 \pm 0.178	0.000	-1.05 \pm 0.200	-1.23 \pm 0.368	-6.86 \pm 3.526 ^c	0.001	-6.86 \pm 3.526 ^c	0.052
Date-of-death								
14 Feb-14 Mar	-1.25 \pm 0.391	0.001	-1.07 \pm 0.417	2.55 \pm 1.673 ^c		0.127		
15 Mar-15 Apr	1.00 \pm 0.262	0.000	1.17 \pm 0.300					
16 Apr-15 May	0.25 ^b		0.10 ^b					
Distance to road								
≤ 400 m	-1.04 \pm 0.298	0.002 ^a	-0.83 \pm 0.283			0.162 ^a		0.274 ^a
401-1,000 m	0.41 \pm 0.246	0.098	0.36 \pm 0.297	-0.55 \pm 0.393 ^d	-0.69 \pm 0.632 ^d	0.162	-0.69 \pm 0.632 ^d	0.274
1,001-2,000 m	0.67 \pm 0.251	0.008	0.66 \pm 0.278	0.55 ^b	0.69 ^b		0.69 ^b	
> 2,000 m	-0.04 ^b		-0.20 ^b					
Distance to human development (km)								
≤ 5 km	-1.36 \pm 0.393	0.000 ^a	-0.87 \pm 0.217 ^e	-0.13 \pm 0.597	-5.15 \pm 4.903	0.822 ^a	-5.15 \pm 4.903	0.293
> 5 km	1.36 ^b			0.13 ^b	5.15 ^b	0.822	5.15 ^b	0.293
Study area identity								
Firehole-Gibbon	0.58 \pm 0.218	0.008 ^a						
Northern Range	-0.58 ^b							

^a P-value for parameter, inclusive of all categories.

^b Coefficient calculated by difference.

^c Parameter estimated for the natural log of Julian date.

^d Parameters estimated for distance-to-road categories ≤ 1,000 and > 1,000 m.

^e Parameter estimated for natural log of distance to primary development (km).

Range study area, even accounting for all other independent effects.

Models for each study area also provided a good fit ($G = 242.6$, 346 df, $P = 1.000$, and $G = 70.3$, 496 df, $P = 1.000$, for the Firehole-Gibbon and Northern Range study areas; Table 4). We did not include elevation in the Firehole-Gibbon model because of the narrow elevational range in this study area. Distance to nearest forest edge also was not significant. Otherwise, probability of carcass use by grizzly bears here was most strongly related to annual carcass abundance (negative), distance to a primary development (negative), and date-of-death (negative for 14 Feb–14 Mar, and positive for 15 Mar–15 Apr). In the Northern Range model, coefficients for distance to nearest forest edge, distance to nearest primary development, distance to nearest road, and date-of-death were not significant. Probability of use was, however, strongly related to edible biomass (positive), carcass abundance (negative), and elevation (positive).

Black Bear versus Grizzly Bear Use.—We investigated the effects of edible carcass biomass, date-of-death, distance to forest edge, distance to primary road, distance to primary development and elevation on the probability that a black bear versus a grizzly bear used a carcass, pooling data from both study areas. Model fit was good ($G = 30.9$, 82 df, $P = 1.0$) although coefficients for edible biomass, distance to nearest road, distance to forest edge, and distance to primary development were not significantly different from zero (Table 4). The probability that a grizzly bear rather than a black bear used a carcass was strongly and positively related to elevation and negatively related to date-of-death; i.e., black bear use was increasingly likely with decreasing elevation and later date-of-death.

Number of Carcasses Used versus Number Available.—The number of carcasses annually used by bears in the Firehole-Gibbon study area increased as the number of carcasses available increased up to 70 (Fig. 8). Above this level use rapidly approached an asymptote of 26 carcasses and increases in availability of carcasses apparently did not result in increases in use. Based on points of inflection for this acute sigmoidal relation, the greatest increase in use per unit increase in availability occurred between 40 and 70 available carcasses. A similar relation was evident for the Northern Range except that

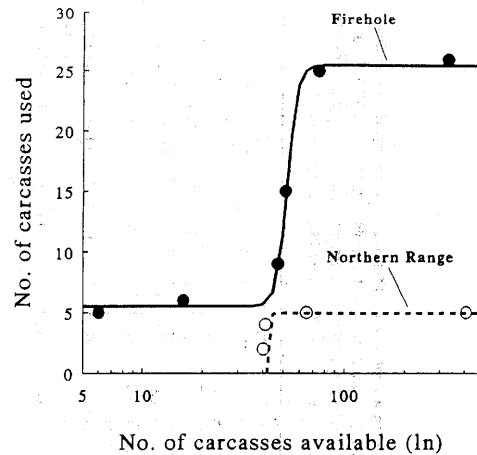


Fig. 8. The relations between number of carcasses used by grizzly bears and the number annually available on ungulate winter ranges in Yellowstone National Park, for the Firehole-Gibbon (1985–90) and Northern Range (1987–90) study areas. Each point denotes a different study year. Models are based on the logistic relation: $\hat{Y} = i + (k/[1 + \exp(a - bx)])$.

the asymptote was much lower (5) compared to the Firehole-Gibbon (26) and little, if any, observed carcass use was predicted to occur at carcass availabilities <40.

DISCUSSION

The rapid rates at which carcasses were consumed during normal winters, especially on the Northern Range, suggest that this negatively affected the use of carrion by scavenging grizzly bears. The probability of finding edible biomass on a carcass was greatly reduced if a grizzly did not find a carcass within the first few days after the animal's death. Thus, the data indicate a high proportion of carcasses used by grizzly bears occurred within 3 days of the animals' deaths.

The greater use of bison compared to elk, and especially deer carcasses, also indicated the importance of slower carcass depletion rates to bears. Bison carcasses remained available for longer periods of time, presumably due to their greater size, allowing more time for discovery by grizzlies. Also, smaller-bodied elk <1 year old and deer were absent from among the carcasses used by grizzlies. Mattson (1997) also concluded that carrion from ungulates that offered ≤ 16 kg (dry wt) of edible biomass were essentially unavailable to radiomarked grizzly bears in the Yellowstone area because of competition from other scavengers.

The importance of slower depletion rates was

highlighted by the frequency with which grizzly bears used ungulates that died in bogs (Green 1994). On the Northern Range, 4 of the 14 carcasses used by bears were extracted during different years from a single bog. These ungulate carcasses were submerged and preserved from midwinter until spring when grizzly bears pulled them onto surrounding banks. In the Firehole-Gibbon study area, 5 of 10 young elk and bison that were first used by grizzly bears more than a week after death had died in bogs or springs. Without preservation in peat and water, these small carcasses probably would not have been available to bears.

The likelihood that grizzly bears used an ungulate carcass during the spring also increased with elevation. This pattern was clear from our carcass observations and was corroborated by the distribution of grizzly bear track sets. This phenomenon may be explained by 3 factors. First, grizzly bears dened at an average elevation of 2,470 m (2,000–3,050 m range) in the Yellowstone area, in the upper elevations of the Northern Range study area and nearer to the Firehole-Gibbon study area (Judd et al. 1986). Carcasses near winter dens were more likely to be found first as grizzlies began foraging in the spring from high elevations. Second, a greater number of larger-bodied bison carcasses were found in the higher elevation Firehole-Gibbon study area compared to the Northern Range study area. Third, we found indications of fewer competing scavengers at higher elevations. Black bears were less likely to forage at higher elevations, and we had reason to suspect coyote densities were much lower at higher elevations (R. Crabtree, pers. commun.; pers. obs.). Fewer scavengers would explain the slower rates of carcass depletion in the higher elevation Firehole-Gibbon study area compared to rates of depletion for the same carcass types on the Northern Range study area.

These potential differences in densities of competing scavengers and numbers of large-bodied bison carcasses may explain why the probability of carcass use by grizzly bears was so much higher in the Firehole-Gibbon compared to the Northern Range study area, even accounting for the effects of elevation. This difference in frequency of scavenging between the northern and western parts of the Yellowstone area also was observed for radiomarked grizzly bears by Mattson (1997), and attributed to differences in coyote densities as well as differ-

ences in availability of other high-quality foods. The influences of competing scavengers may thus explain why edible biomass had a stronger effect on the probability that a carcass was used by grizzly bears on the Northern Range compared to the Firehole-Gibbon winter range. Differences in competition for carrion also may explain the major difference in number of carcasses used on each range as a function of carcass availability.

The acute sigmoidal relation between annual availability and use of carcasses by grizzly bears offered several insights. Demand was apparently either close to or at saturation during 2 of 6 and 2 of 4 years in the Firehole-Gibbon and Northern Range study areas. These years included 1989 in both study areas, following massive dieoffs caused by the drought and wildfires of 1988 (Singer et al. 1989), in accordance with heavy use of ungulates during 1989 by radiomarked grizzly bears (Mattson 1997). These acute relations were also much like the ones observed between the availability and use of whitebark pine (*Pinus albicaulis*) seeds by grizzly bears in the Yellowstone ecosystem (Mattson and Reinhart 1994). In general, this type of relation betokens major annual shifts in diet and a high degree of selectivity among major foods and the habitats where these foods are obtained (Real 1977).

Black bears and grizzly bears appeared to be segregated primarily by elevation. In more concrete terms, black bears did not often forage above the juncture of the Yellowstone and Lamar rivers or in the Firehole-Gibbon area—in areas where grizzly bears were commonly active. Black bears also tended to more often use carcasses later in the spring, when carcasses with edible biomass were less common. This type of segregation was also observed on cutthroat trout (*Oncorhynchus clarki*) spawning streams tributary to Yellowstone Lake, where black bears foraged more often near humans or on less productive streams where large lone grizzly bears were less active (Reinhart and Mattson 1990). Whether black bears were disadvantaged by this spatial and temporal segregation is not clear. However, these results and previous observations of sympatric conflict between the 2 species (Arnold 1930, Hornocker 1962, Mattson et al. 1992) suggest that black bears may have avoided grizzly bears and settled for use of somewhat less productive habitat.

Humans clearly affected the behavior of grizzlies. Controlling for other influences that normally plague radiotelemetry studies and single factor analyses, grizzly bears substantially underused carcasses within 400 m of roads and within 5 km of major recreational developments in the Firehole-Gibbon study area. Beyond these zones, virtually all the carcasses available after mid-March were used by grizzly bears. Human influences were more equivocal on the Northern Range, but patterns here were consistent with those observed in the Firehole-Gibbon study area. In addition to the small sample of carcasses used by grizzly bears, it is also possible that results here reflected the constraints imposed upon grizzly bears by high levels of competition from other scavengers. Even so, the one carcass used by a grizzly bear within 400 m of a road in this area was the victim of bear predation and thus not indicative of the more common scavenging behavior. These results are part of a growing body of research that shows grizzly bears avoiding areas near human facilities (Archibald et al. 1987, Mattson et al. 1987, McLellan and Shackleton 1988, Kasworm and Manley 1990, Reinhart and Mattson 1990, Aune 1994).

The concentration of carcasses on geothermally influenced soils helps explain the higher carcass densities near roads in the Firehole-Gibbon study area. Road locations in Yellowstone National Park were "selected with a view of securing easy grades and proximity to as many as possible of the features of interest near which it passes" (Chittenden 1892). The "features of interest" in these winter ranges were undoubtedly the geothermal activity that, perhaps unintentionally, coincided with ungulate winter range and habitats thereby important to grizzly bears. The apparent severity of human effects on bears in this study area was thus a result of historical priorities and part of a heritage of conflict brought about by the U.S. National Park Service's dual mandate to "conserve" and "provide for the [public's] enjoyment" (Wright 1992).

MANAGEMENT IMPLICATIONS

High-elevation ungulate winter ranges are important to the spring use of carrion by grizzly bears in Yellowstone National Park. The current Firehole Bear Management Area closure (Nat. Park Serv. 1994) serves to discourage human disturbance of grizzly bears using carrion that is

distant from roads, but does not adequately achieve the objective of preventing human-caused displacement of bears from prime food sources (Gunther 1994). Other closures of roads, boardwalks, and trails in and around geothermal basins from April to mid-May could allow for increased grizzly bear use of carrion. This opportunity is emphasized by the presence of long-persistent carrion in the form of adult bison near currently active human facilities. Elsewhere, grizzly bears could benefit by closing or continuing to close smaller ungulate winter ranges in the interior of the Park and bogs that serve as traps for elk and bison to human activity during the spring. Movement of carcasses away from roads, boardwalks and trails to sites remote from human activity (Craighead et al. 1995) and at higher elevations could serve as an alternative to closures.

Grizzly bear use of carrion also is affected by the number of winter-killed ungulates on winter ranges. Given that mule deer carcasses are essentially unused by grizzly bears, variation in the numbers of elk and especially bison that die are likely to have the greatest effects on bears. The amount of edible biomass on dead animals that is actually available to grizzly bears is probably also affected by variation in the numbers of competing scavengers. Yellowstone's grizzly bears likely have been, and will continue to be, affected by changes in numbers and sex and age compositions of elk and bison herds, and by changes in the numbers of coyotes, black bears, and, presumably, wolves. Events that favor fewer competing scavengers and greater numbers of vulnerable adult ungulates likely will benefit grizzly bears in the Yellowstone ecosystem.

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Received 15 June 1996.

Accepted 17 July 1997.

Associate Editor: McDonald.