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REVIEW AND SYNTHESIS

Grizzly Bears & Ungulates in the Yellowstone Ecosystem

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Abstract *Meat from ungulates is a high-quality bear food. Because of foraging efficiencies, this is especially true of meat available in large volumes from concentrated sources. Given these two axioms, meat from bison—the largest-bodied of any surviving Holocene ungulates—is predictably of considerable value to grizzly bears wherever they have access to this food. Data from scientific investigations spanning nearly 60 years affirm not only the importance of meat to Yellowstone's grizzly bears, but more specifically the disproportionate importance of meat from bison carcasses. Grizzly bears obtain more meat from bison carcasses and are more likely to exploit such a carcass compared to remains of elk. Yellowstone's grizzly bears are increasingly reliant on meat from ungulates because of declines in other important foods. Dramatic increases in conflicts over livestock and hunter-killed elk suggest that grizzlies are more often seeking meat under circumstances that bring them into conflict with humans. The one exception is bison from which tissue is obtained under circumstances that foster survival of involved bears.*

Keywords Elk, Bison, *Ursus arctos*, *Cervus Canadensis*, *Bison bison*, scavenging, predation

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1. Introduction

In this paper, I provide a detailed examination of relations between grizzly bears (*Ursus arctos*) and ungulates (i.e., large hooved herbivores) in the Yellowstone ecosystem of Wyoming and Montana. I give special emphasis to relations between bears and bison (*Bison bison*) in this last place on Earth where both still co-occur. Bison and grizzlies were extirpated by European settlers from most of their pre-contact distribution in the western United States between 1800 and 1900, amounting to a 97% decline for grizzly bears and a 99% decline for bison [1,2]. The joint remnants in Yellowstone constitute a mere 1% of what once existed in the Great Plains, Rocky Mountains, and northern Great Basin, entailing what I speculate to have been an intimate, complex, and important triad of relations involving bears, bison, and native peoples [3,4]. Here, I elaborate on what we have been fortunate enough to learn about contemporary relations between grizzly bears, bison, and other ungulates in Yellowstone, which is foundational to understanding relations between especially bison and grizzlies during the last 30,000+ years in areas that encompassed much of ice-free western North America [3].

2. Meat as Bear Food

Meat—comprised of muscle, adipose tissue, and fascia—is among the highest quality grizzly bear foods [5]. It is calorically rich and thoroughly digested—typically greater than 90%. Depending on the exact composition, it is efficiently converted to either lean body mass or body fat. Fat content of meat is predictably higher during late summer into fall on the herbivores typically exploited by bears, at a time when gaining body fat is key to survival of bears during the following winter and spring. Although efficiency of gain in body mass declines for bears when average dietary protein exceeds roughly 20%, this holds only when all else is equal. Bears with unlimited access to meat can gain 1-4 kg per day, with absolute gains increasing as mass of the involved bear increases. By contrast, peak rates of gain for bears on diets of fruits or foliage are around 0.5-1 kg per day, but only for bears weighing between 50 and 150 kg. Larger bears may lose weight on fruit diets, and almost invariably lose weight when eating foliage, primarily because of protein deficiencies and the mounting inefficiencies of foraging relative to base metabolic needs. (For more detail, see [5]).

Photo by *Interagency Grizzly Bear Study Team*

Meat from bison is exceptional because it is available in such large quantities to any bear fortunate enough to possess some part of a fresh bison carcass. Adult female bison typically weigh more than 400 kg, of which roughly 100+ kg is edible dry mass [6]. The same figures for bull bison are 600-800 kg live weight and 150-200+ kg edible dry weight. By contrast, edible dry weight on adult elk (*Cervus canadensis*) is typically between 30-95 kg, and, on an adult mule deer (*Odocoileus hemionus*), closer to 4 kg. Of the edible mass on a bison carcass, fat varies from roughly 15% during spring to 40+% during late summer and fall [7]. Percent protein correspondingly declines from roughly 80% to 50% during the growing season. Given these trends, bison meat consumed by bears from spring carrion predictably contributes more to growth of lean body mass rather than body fat, whereas the opposite is predictably true during late summer at a time when bears are feeding most heavily (i.e., during hyperphagia).

Bears are not the best of predators. They have comparatively robust forelimbs and associated muscles and skeletal anchors that facilitate, in turn, dexterous but powerful use of their forepaws for digging, climbing, and grasping [8]. As a corollary, they have a plantigrade gait, which results in bears being comparatively slow and inefficient runners for their size. They are thus more successful as ambush predators rather than cursors, and, as predators, they can efficiently dispatch prey as large as adult elk or even moose at short range [9]. More often, though, grizzly bears prey on newborn moose and elk calves prior to when they are fully mobile.

Illustration by *Charles M. Russell* based on an eye-witness account by William Allen. Only one other instance is known of predation by a grizzly bear on an adult bison.

By contrast, grizzly bears in the Yellowstone ecosystem only rarely prey on bison. Most of the meat they obtain from bison carcasses is in the form of carrion from animals that died over-winter, cows dying during spring from birthing complications, bulls dying during late summer and fall from injuries sustained during the rut or, increasingly, by displacing wolves from bison kills. During 1977-1992, the only period for which we have detailed information, grizzly bears obtained only 4% of the bison meat that they ate by outright predation, in contrast to 39% from mule deer, 44% from elk, and 46% from moose [6]. Grizzly bears occasionally do prey on bison, including calves [10], yearlings [6], and the very rare adult [11], but as an exception rather than a rule. Even bison calves are comparatively safe from bear predation given the tendency of herd-dwelling bison bulls and cows to collectively defend their offspring [12]. Although aggressive, cow moose are solitary, whereas less aggressive but herd-dwelling cow elk rarely mob attacking bears [13,14].

Still from video by *Dale Bohlke*

3. Importance of Meat to Yellowstone Bears

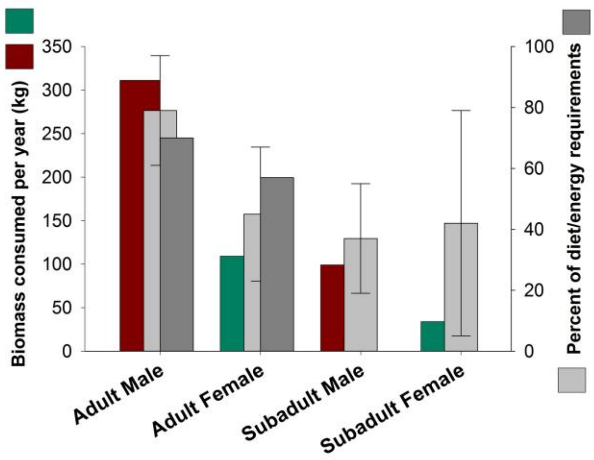


Figure 1. Comparative consumption of meat from ungulates by grizzly bears in the Yellowstone ecosystem, differentiated by sex- and age-class (adults are >4-yrs old; subadults, >2-yrs old). The burgundy and turquoise bars denote estimated amounts of meat consumed per year by males and females, respectively (scaled to the left-hand y axis). The light and dark gray bars denote the proportion of total annual energy obtained from terrestrial meat by bears of different sex- and age-classes, with the dark gray bars corresponding to percent of energy requirements, and the light gray bars, percent of total ingested energy (scaled to the right-hand y axis).

Grizzly bears in the Yellowstone ecosystem obtain a substantial portion of their energy and nutrients from eating meat, although this fraction varies by orders-of-magnitude among different sex- and age-classes, and has varied over time (see below). Figure 1 summarizes various historical estimates of meat consumed by Yellowstone's grizzly bears, including contributions to annual energy budgets [6,15,16]. All these estimates suggest that adult males eat (or ate) by far the most meat, with other bears falling within a lesser range.

More specifically, estimates from 1977-1992 suggest that the average adult male ate >300 kg of meat, dry weight, per year, accounting for roughly 70% of their total energetic needs [6]. Figures for adult females were roughly 100 kg of meat, meeting 50-60% of energetic needs—similar to values for subadult males. Recent estimates, shown by light gray bars in Figure 1, are remarkably conciliant with those from 10-30 years earlier [16].

Although Yellowstone's grizzly bears are not among the most carnivorous of grizzly bears in North America, meat does constitute an important food [15,17,18]. On a population basis, dietary meat from terrestrial sources averages continent-wide around 25% [18], which places Yellowstone well within the upper half of populations insofar as reliance on non-marine meat is concerned. At >40% population-wide, Yellowstone only ranks less than those populations in the arctic and sub-arctic that rely on caribou (*Rangifer tarandus*) and arctic ground squirrels (*Spermophilus parryii*) as primary foods [18,19]. Generally, populations occupying drier flatter environments tend to rely more on terrestrial meat [19], which is consistent with comparatively dry continental conditions in Yellowstone, as well as conditions prevalent in the Great Plains, northern Great Basin, and lower elevations of the Rocky Mountains, where I speculate that bison were once a critically important food for grizzly bears prior to widespread extirpations of both bison and bears between 1800 and 1900 [3].

Which species of ungulates have contributed most to Yellowstone's grizzly bear diet? Calculations from data collected during 1977-1992 [6] suggest that bears got most meat from elk (53%), next most from bison (24%), and a surprisingly large amount from moose (*Alces alces*; 18%). Given the abundance of each species in the ecosystem at that time, grizzly bears obtained 3-times as much meat from bison as would be expected by their numbers, and an astounding 20-times more from moose. Unfortunately, a more recent break-down of species-specific contributions is not available for lack of sustained intensive field investigations during recent decades. However, for reasons that I describe later, the fractional contribution of bison has likely increased along with a decline in contributions by both elk and moose.

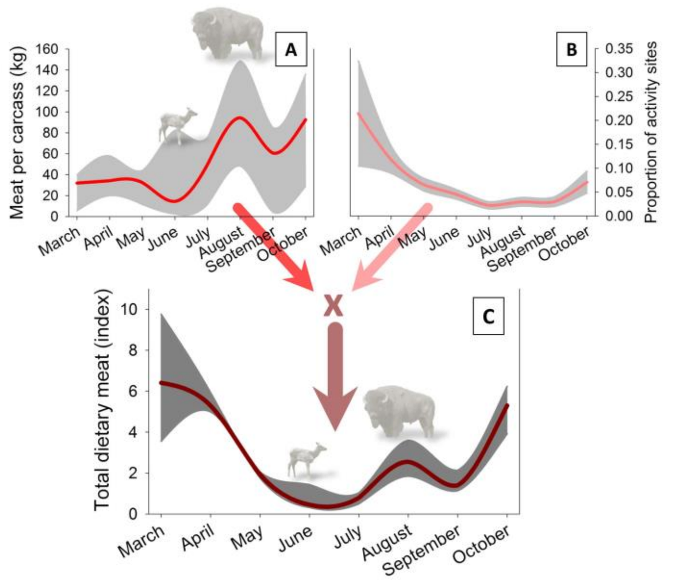


Figure 2. Aggregate monthly consumption of meat from all ungulate species by Yellowstone grizzly bears during 1977-1992. Panel A shows average mass consumed from individual carcasses; Panel B, relative frequency of exploitation of ungulates; and Panel C, total consumed biomass as a function of frequency and per carcass biomass.

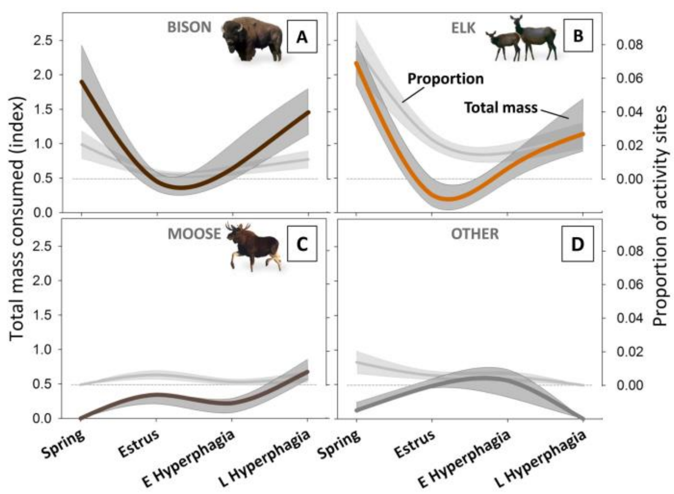


Figure 3. Seasonal consumption of meat from different ungulate species by Yellowstone grizzly bears during 1977-1992. The lighter gray trend lines and associated uncertainty intervals represent frequency of exploitation as a fraction of total bear activity. The darker colored trend lines and associated dark gray uncertainty intervals represents consumed biomass (an index calculated as frequency times mean tissue consumed per investigated carcass). Uncertainty intervals for consumed biomass were generated by averaging values calculated from multiple joint randomly-drawn values from the intervals associated with proportional frequency and per carcass consumed biomass.

3.1 Seasonal Patterns

Seasonal patterns of meat consumption by Yellowstone's bears are relatively consistent from one year to the next. Most years there is a peak in consumption during spring, coincident with peak availability of carrion on ungulate winter ranges, and a later peak in consumption during late summer-early fall, focused on exploitation of bulls coincident with or closely following rutting activity (Figure 2C) [20,21]. The minor peak during August (Figure 2A) reflects consumption of bull bison that died during the rut, and the substantial amounts of biomass available from such a carcass (see below). In general, the average amount eaten on any given carcass peaks during August-October [20]. By contrast, average amounts consumed per carcass are least during June, coincident with peak exploitation of small-bodied elk calves.

Consumption of both bison and elk (Figure 3) closely follow aggregate seasonal patterns, although consumption of moose lacks a spring peak. The big difference in patterns between bison and elk arise from differences in body mass. The seasonal frequency with which grizzlies exploit bison is consistently less than the frequency with which they exploit elk, although seasonal amounts of consumed biomass are similar because of the offset introduced by much larger bison carcasses (see above and immediately below).

3.2 Differences Among Carcasses

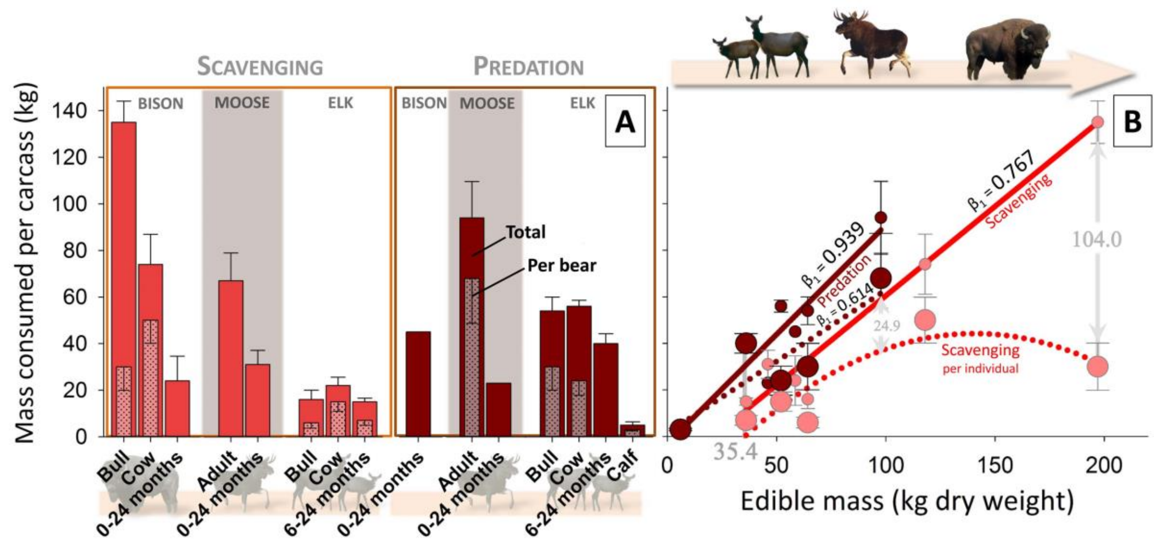


Figure 4. Average (±SE) amounts of meat, dry weight, consumed by Yellowstone grizzly bears from individual carcasses, differentiating species and sex- age-classes of ungulates as well as scavenging versus predation. Total amounts eaten by all involved bears are denoted by the broader bars behind; amounts eaten by individual involved bears are shown by the narrower lighter-shaded bars in front.

Figure 5. Relations between total meat consumed per carcass and amount of edible biomass available, differentiating scavenging from predation and amounts consumed by individual versus all involved bears. Solid trend lines are for total mass consumed, dashed trend lines for mass per individual bear. Dot sizes are proportional to

Figures 4 and 5, immediately above, show the mass consumed by Yellowstone grizzly bears from different types of carcasses, differentiating bison, moose, and elk, whether the carcass was scavenged or obtained by outright predation, and a break-down of biomass consumed per involved bear versus the total consumed by all bears [6]. In Figure 4, patterns are shown relative to species and sex- and age-class of the exploited carcass. In Figure 5, biomass consumed is related to biomass available on any given type of carcass, again differentiating scavenging from predation.

The patterns are not subtle nor surprising. More biomass was consumed from larger carcasses, with more mass obtained when an animal was predated versus scavenged. Of all carcass types, whether predated or scavenged, the most mass was obtained by bears, *in toto*, from bull bison, with comparable amounts obtained from cow bison and predated and scavenged adult moose, followed closely by amounts from predated adult elk.

No predation on adult bison was documented during 1977-1992 [6], and has been rare since [11], which makes this behavior largely extraneous. At some point, roughly at the size of adult bison, potential prey animals become so large and (collectively) aggressive as to effectively preclude predation by grizzly bears. However, among moose and elk, those animals that were killed outright consistently served up more biomass compared to those that were scavenged, especially when reckoned for an individual bear. Interestingly, as carcass size increased, the disparity between volumes obtained by predation and scavenging generally increased for individual grizzlies.

None of these differences is surprising, whether between predated and scavenged carcasses, magnitudes of this difference at different carcass sizes, or differences in portions obtained by individual bears. All these disparities can be explained by competition or lack thereof. Any animal that is killed outright by a bear will offer the involved bear not only first servings, but also a chance to sequester the carcass to minimize the dissemination of odors that might attract other scavengers. Without predation, the time necessarily involved for most bears to detect most carcasses allows for other scavengers (e.g., coyotes and ravens) to detect and consume some portion of the edibles [22,23]. Moreover, larger carcasses (e.g., those of bull and cow bison) will persist longer [22] and, along with greater persistence, more likely attract other scavenging bears; hence a slight decrease in the amount consumed by any individual bear from a bull bison carcass versus a cow bison carcass despite the greater total mass on a bull.

4. Annual Consumption of Carrion by Bears

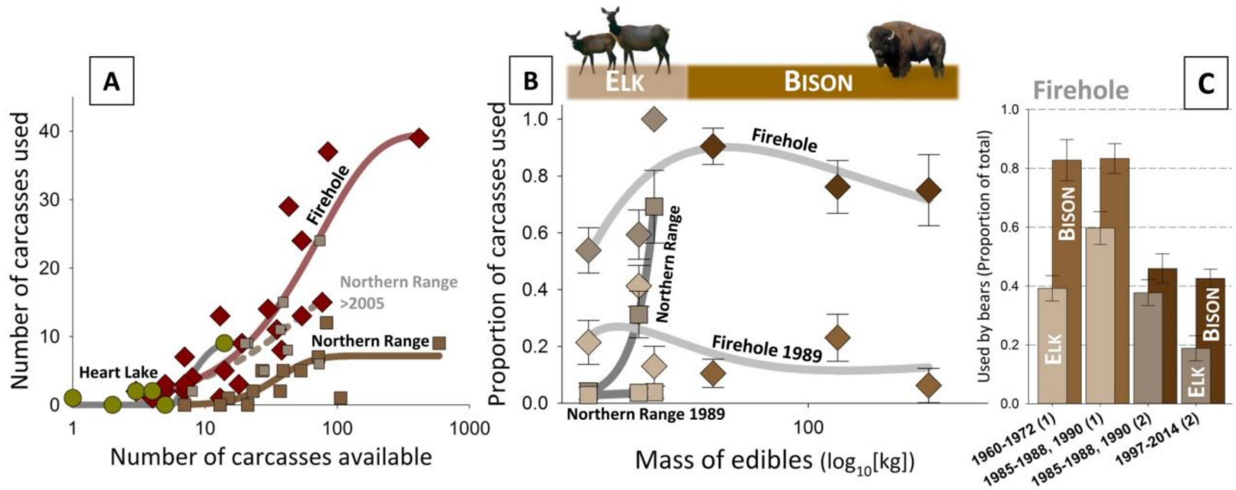


Figure 6. Relations between levels of spring-time carcass exploitation by scavenging bears on winter ungulate ranges and various explanatory factors, including numbers of available carcasses (A), size of the carcass (B), and, related, whether bison or elk (C)—differentiated by study area (Northern Range, Firehole, and Heart Lake), study period (1960-1972; 1985-1990; 1997-2014), and a year of carrion glut (1989) versus the rest (1985-1988, 1990). All these data were collected along transects monitored for various durations during the spring.

Figure 6 shows the effects of various factors on the probability that a carcass would have been scavenged by either a black or grizzly bear on ungulate winter ranges during spring in the Yellowstone ecosystem. These winter ranges include the Northern Range centered on the Lamar and Yellowstone Rivers, geothermally-influenced areas centered on the Firehole and Gibbon Rivers, and a smaller enclave of geothermally-warmed habitat along Witch Creek and around Heart Lake in southern Yellowstone National Park. Most of these data were collected from transects that were monitored during two study periods, the earlier lasting 1985-1990 [22,23] and the latter 1997-2014 [e.g.,24]. Given that consumption of tissue from bison carcasses by bears is almost wholly by scavenging, these results are particularly relevant to relations between bears and bison.

Panel A shows relations between numbers of carcasses available and numbers scavenged by bears, differentiated by winter range and, for the Northern Range, by whether data were collected before or after 2005 [22,24]. A couple of patterns are worth noting. First, numbers of exploited carcasses reach a plateau once available numbers much exceed 100, at least on monitored transects. Such an asymptote suggests a saturation of demand, at least by scavenging bears. The second pattern pertains to differences between study periods on the Northern Range. Data from later years suggest a response curve much like that observed in the Firehole-Gibbon and Heart Lake study areas, whereas data from before suggest less bear activity at any given level of carrion availability. This difference between time periods on the Northern Range could be interpreted as suggesting that spring bear activity (and densities?) on the Northern Range had increased between 2004 and 2005 to levels comparable to the other two study areas. Foreshadowing other results that I present later, this increase could simply be a result of proportional and absolute increases in numbers of bison carcasses on the Northern Range. Such increases would predictably create a richer and more attractive foraging environment for bears given the greater biomass available on bison versus elk carcasses (see above).

Panel B in Figure 6 shows the likelihood that a given carcass would have been exploited by a bear as a function of, first, the biomass available per carcass and, second, whether the year was one of glut (1989) or not (all other years) [6,22,23]. The first and perhaps most obvious pattern in these relations is consistent with Panel A; probabilities that any given carcass would have been scavenged by a bear were far less during a glut, regardless of carcass size. Carrion was much more abundant during spring of 1989 compared to any other year that winter ranges were monitored [22]. This spring followed a particularly harsh winter on top of severe drought and fires during 1988 that deprived elk and bison of forage during the concurrent summer and following winter. We haven't seen a similar combination of circumstances before or since.

Secondary to this abundance-driven pattern, bears were more likely to scavenge larger versus smaller carcasses (i.e., bison versus elk), but peaking with carcasses the size of cow bison. Interestingly, probabilities of exploitation dropped slightly for bull bison carcasses, despite being much larger in size. I speculate that this anomaly was a result of handling costs and the greater likelihood of competition from other bears (see above). The hide on a bull bison is the thickest of any on a carcass in the Yellowstone ecosystem, entailing energetic costs for a scavenger. In fact, I have seen bull bison essentially mummify if bears have not ripped open the hide. No scavenger other than wolves can apparently otherwise gain access to the edibles within.

Finally, Panel C in Figure 6 reinforces the comparative importance of bison versus elk carcasses to scavenging bears, but encompassing three different studies in the Firehole-Gibbon area spanning roughly 55 years—1960 to 2014 [23,24,25]. The earliest study was undertaken by John and Frank Craighead 1960-1972 [25]. Given a difference in methods between the earliest and most recent studies (i.e., transects and time monitored), the middle study, 1985-1990, was recalibrated to allow comparison with both (shown as 1985-1988, 1990 (1) and (2)). The seminal patterns are, first, that, compared to elk carcasses, bison carcasses have consistently been more often scavenged by bears and, second, elk carcasses were more likely to be scavenged during the middle compared to either the earlier or later years. At this point, the heavier exploitation of bison carcasses needs no explanation. Differences in exploitation of elk carcasses between study periods remain bit of a mystery.

5. Availability of Carrion During Spring

The availability of carrion to bears on ungulate winter ranges in Yellowstone National Park varies substantially between March 1st and May 15th, the period during which virtually all scavenging by bears typically occurs. Surveys undertaken during spring of 1985-1990 [24] provide perhaps the most detailed information currently available on patterns of ungulate die-off and associated levels of grizzly bear activity on these winter ranges, primarily thanks to the efforts of Gerry Green and Jeff Henry (Figure 7).

During the "normal" years of 1985-1988 and 1990, peak post-February ungulate die-offs consistently occurred during the last half of March and the first half of April, coincident with peak die-offs of cow elk and short-yearlings. Among bison, die-offs during early April were driven more by cows and bulls, in contrast to March die-offs comprised of proportionately more short-yearlings.

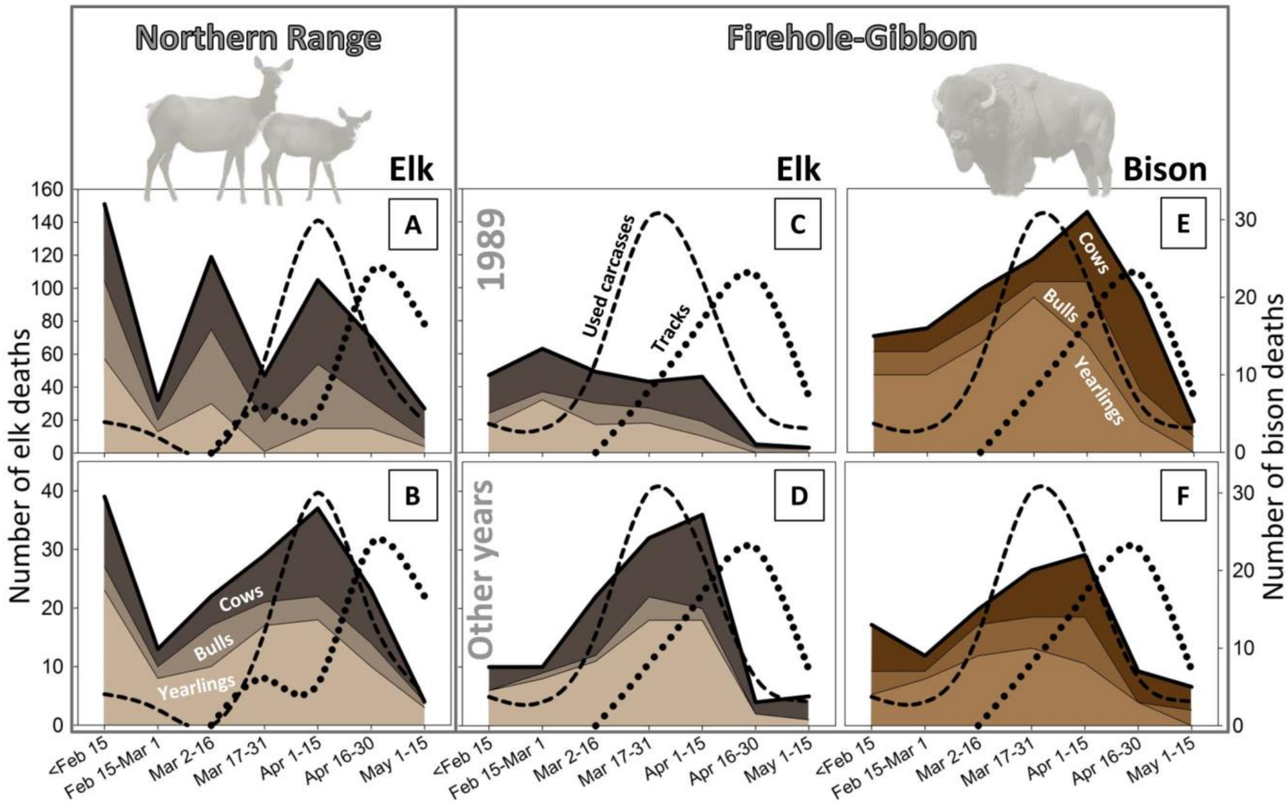


Figure 7. Biweekly availability of carcasses on winter ranges in Yellowstone National Park, differentiating the Northern Range from the Firehole-Gibbon area; elk from bison; different sex and age-classes (cows v bulls v short-yearling and yearlings); and the extraordinary die-off- during spring of 1989 from all other years (1985-1988 and 1990; notice the difference in scales top and bottom on the left). Levels of bear activity averaged over all years are also shown for the Northern Range and Firehole-Gibbon area, both as numbers of carcasses exploited (dashed line) and numbers of tracks encountered (dotted lines).

The heavy die-off of ungulates during 1989 exhibited both similarities and differences compared to other years. On the Northern Range, elk die-offs consisted of proportionately many more adults, especially bulls, as well as an anomalous peak during early April. On the Firehole-Gibbon winter range, comparative biweekly levels of die-off were similar between 1989 and other years, except that short-yearlings comprised a greater fraction of the total. Among elk, total die-offs tended to be concentrated earlier in the spring, most notably a peak in deaths of short-yearlings during late February. Broadly, elk were affected more than bison by the severe conditions of 1988-1989, including not only a proportionately much large die-off, but also a concentration of those deaths earlier during spring.

Annually-averaged levels of grizzly bear activity on the surveyed winter ranges closely mirrored availability of carrion. Peak exploitation of carcasses during March 15th-April 15th on the Firehole-Gibbon winter range and April 1st-April 15th on the Northern Range closely matched aggregate die-offs in these respective areas. Interestingly, peaks in numbers of detected bear tracks occurred between two and four weeks later, which could simply be a consequence of greater snow cover and resulting ephemerality of tracks prior to mid-April. As a bottom line, this match of exploitation to availability is yet one more piece of evidence suggesting that bears are efficient foragers.

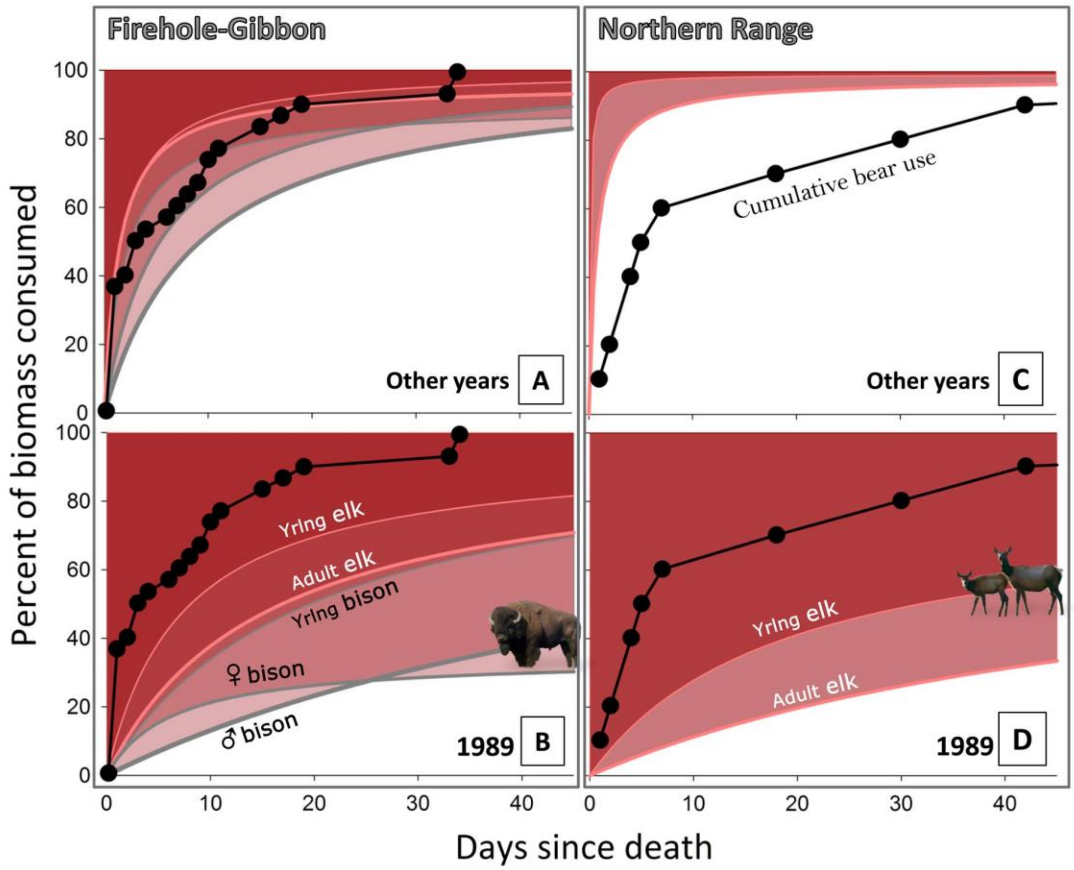


Figure 8. Trends in consumption or wastage of edibles on carcasses observed on winter-range transects as a function of days elapsed since estimated time of death. The Northern Range is differentiated from the Firehole-Gibbon winter range, and the heavy die-offs of 1989 from all other years. Trend lines are fit to different species (bison v elk) and sex- and age-classes. Various shades of red are proportional to amounts of edibles remaining on any given type of carcass. Cumulative observations of bear scavenging on carcasses, aggregated over all years are shown as black dots and lines, differentiating the Northern Range from the Firehole-Gibbon winter ranges.

Figure 8 recasts the information presented in Figure 7, but with an emphasis on the effects of time-since-death on attrition of edible biomass and related odds that a bear would have found and benefited from any given carcass. Again, the glut conditions of 1989 (Panels B and D) are differentiated from all other years (i.e., 1985-1988 and 1990; Panels A and C), along with the Northern Range from the Firehole-Gibbon, and sex- and age-classes ungulates species from each other. The various trend lines for each type of ungulate are fitted to data from individual carcasses that were monitored to estimate percent consumption of edible biomass (y-axis) as a function of estimated days since death (x-axis). As companion information, the cumulative exploitation of carcasses by bears, aggregated over all years (the black dots and line), is also shown as a function of days since death.

The patterns and associated implications for bears are stark. The likelihood that a carcass would have been detected and exploited by a bear culminated only >10-20 days post-death. Yet, during "normal" years on the Northern Range, >80% of edibles had been consumed by scavengers within 2-5 days of an elk's death—most of this by coyotes and birds. Bears were clearly at a disadvantage in competition with other scavengers for remains of elk on the Northern Range during most years. On the other hand, there was such a glut of carrion on elk carcasses during spring of 1989 that most of the edibles went unused by vertebrate scavengers, including bears.

The relations shown in Figure 8 perhaps highlight more than any other the extent to which bison carcasses constitute a superior resource for bears, especially in contrast to elk. Even during "normal" years, bears fared well when exploiting bison carrion on the Firehole-Gibbon winter range, reflected in a close match between likelihood of exploitation and attrition of edibles; 80% loss occurred roughly by 20-40+ days post-death—10-times longer compared to elk on the Northern Range. Cow and bull bison were the most likely of any to offer a scavenging bears substantial amounts of edible biomass, even after 20-30 days of availability to other scavengers. And, of course, during 1989, bison carrion, like that of elk, went largely unused. Interestingly, short-yearling elk on the Firehole-Gibbon winter range were the only carcass type to be more-or-less thoroughly exploited during 1989.

6. Annual Trends in Availability of Ungulates

The abundance of native ungulates in the Yellowstone ecosystem has changed dramatically during the last 30-35 years—between roughly 1980 and 2015. Elk have declined, in places precipitously. Moose have declined as well, largely synchronous with declines in elk. Bison numbers have varied, but with net increase when reckoned for the entire ecosystem. Figure 9 shows trends for all of the elk and bison populations in occupied grizzly bear habitat for which there is longer-term data [e.g.,26-32], registered against the spatial distribution of the referenced herds [30,33,34]. Population estimates are shown are red dots or lines and, where interpolation was needed, as dashed trend lines. The main distribution of bison is shown in brown, with core distribution as darkest brown. For reference, documented instances where grizzly bears fed on ungulates during 1977-1992 [6] are shown as black dots superimposed on ungulate distributions. The only large herds without readily available longer-term trend data are elk in the Clark's Fork and Cody areas, although migratory elements of the Clark's Fork herd are known to have declined, whereas non-migratory elements occupying areas outside of core grizzly bear distribution have increased [34].

The basic thesis of Figure 9 is unambiguous. All the elk herds have experienced declines since the mid-1990s (also the Clark's Fork herd, see immediately above), with declines most dramatic on the Northern Range and in the Firehole and more modest for the Jackson herd, although clearly evident. Trends for bison populations have been mixed, with sustained dramatic increases for the Northern Range herd, and an oscillating decline during the late-1990s, increase during the early 2000s, and subsequent decline for the Central bison herd. Of relevance to relations between grizzly bears and ungulates, notice that known historical instances of grizzly bear feeding are disproportionately concentrated in areas with bison, consistent with a reoccurring theme of disproportionate importance for this ungulate species.

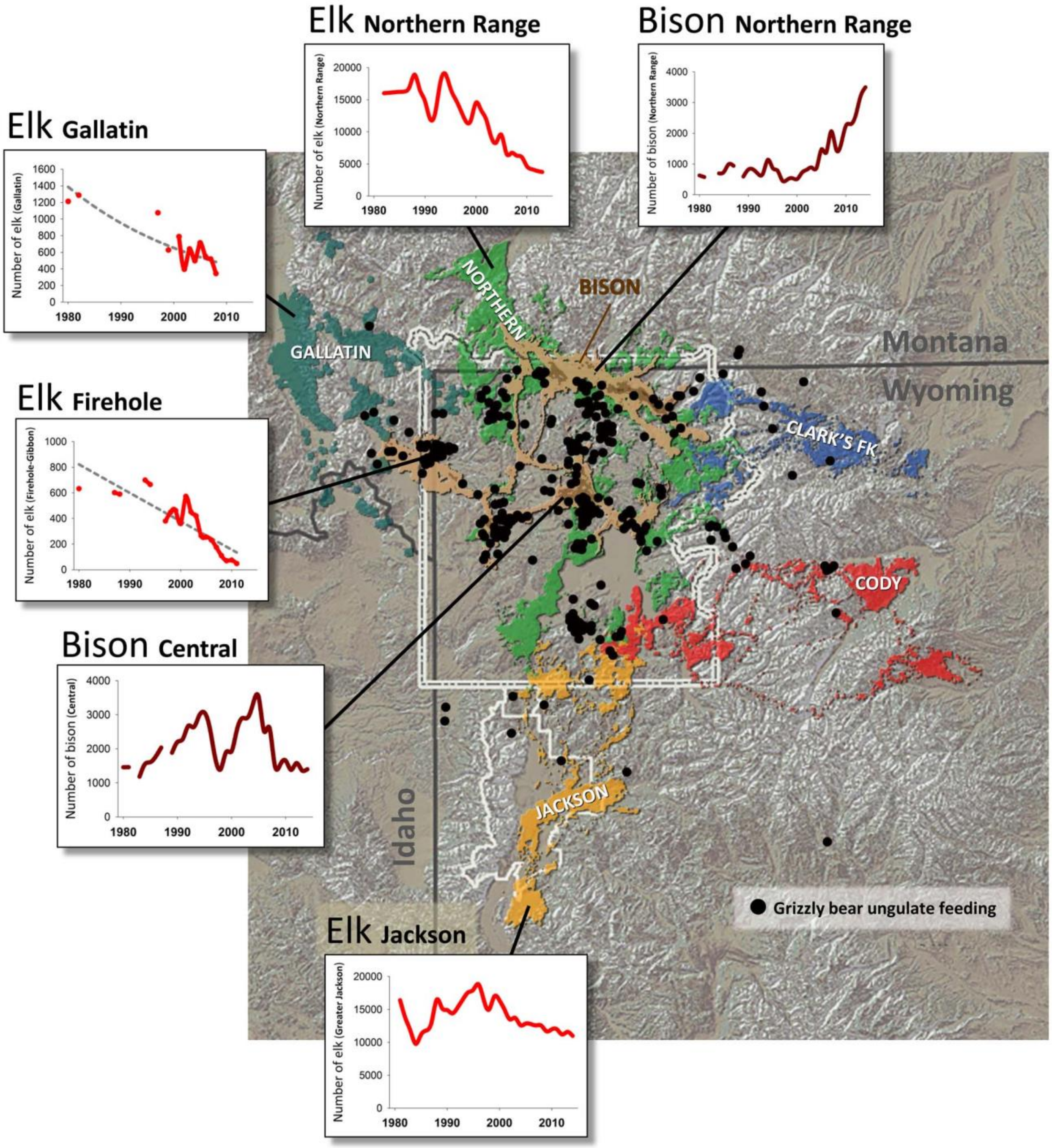


Figure 9. Annual trends and geospatial distribution of elk and bison herds in the Yellowstone ecosystem. Annual population estimates are shown as red or brown dots and lines. Where needed, interpolated trends are shown as dashed lines. Movements of radio-marked elk from each herd are shown as different colors. The main distribution of bison is shown in brown, with core distribution in dark brown. Known locations where grizzly bears fed on an ungulate carcass during 1977-1992 are shown as black dots.

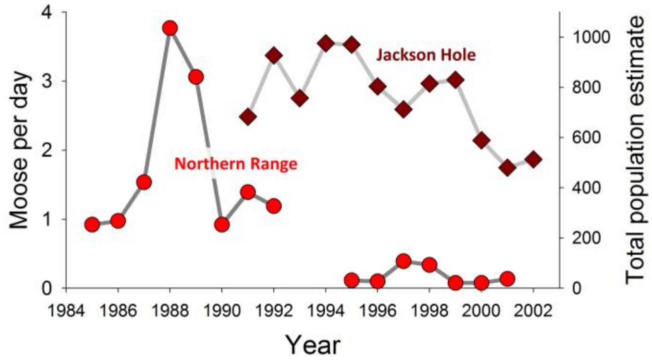


Figure 10. Trends for moose populations on the Northern Range (red line) and Jackson Hole area (burgundy line), 1984-2002. Trend for Northern Range moose is based on an index of moose observed per day of effort.

Moose are also important to grizzly bears in Yellowstone, emphatically so because of the historical consumption of meat from moose by bears 20-fold more than expected by moose numbers (see above). Figure 10 shows trends or trend indicators for two of the larger moose populations in the Yellowstone ecosystem [35,36]. Like elk on Northern Range, sympatric moose here exhibited a sharp decline during the winter of 1988-1989, followed by further sustained declines resulting in near extirpation. Moose in the Jackson Hole have fared better, but gone into decline since 1999.

Panels A and C in Figure 11 on the next page consolidate the various herd-specific estimates for elk and bison into a single trend for total populations of each in areas occupied by grizzly bears in the Yellowstone ecosystem. Panels B and D show concurrent trends in numbers of elk and bison carcasses detected on survey routes monitored annually on winter ranges in Yellowstone National Park [23,24]—which, as per results presented above, is especially relevant to Yellowstone's bears. The aggregate trends are clear. Elk numbers ecosystem-wide have declined substantially, as has elk carrion on winter ranges, especially when reckoned against abundance during the late-1980s. By contrast, bison numbers have increased, although trends in numbers of bison carcasses on winter ranges are more ambiguous, including a suggestion of decline since the late-1980s, but stasis since 1997.

Figure 12 on the following page as well lends emphasis to aspects of these trends, including the emergence of bison as an increasingly important source of meat. Put succinctly, while rates of carcass detection have declined (Figure 12A), the proportion of these carcasses that are bison has increased substantially (Panel B). Moreover, the trend towards increasing proportional representation of bison amongst carcasses available to bears goes back to the 1960s [25]. Proportions of bison have increased dramatically and consistently in the Firehole-Gibbon area, which has been subject to the most sustained monitoring of any winter range in the Yellowstone ecosystem.

Overall, bison have predictably increased in importance as a source of meat for Yellowstone's grizzly bears given declines in elk, elk carrion, and moose.

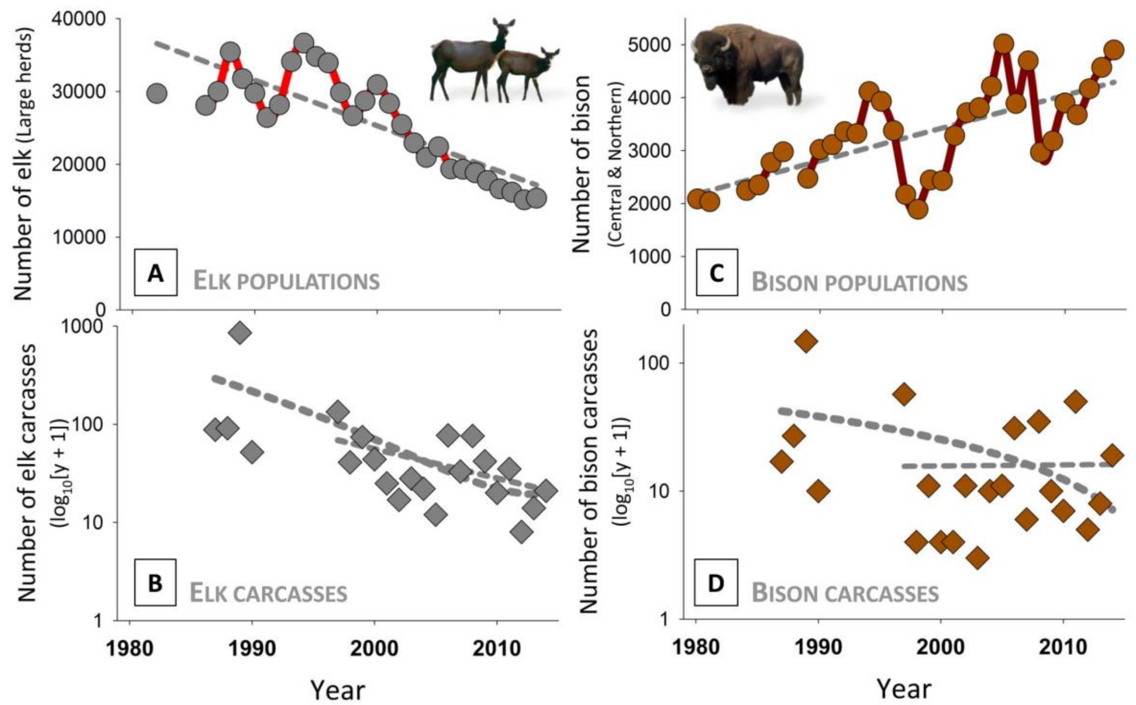


Figure 11. Aggregate numbers of elk (A) and bison (C) in Yellowstone's occupied grizzly bear habitat, along with trends in numbers of elk carcasses (B) and bison carcasses (D) on transects surveyed during spring in Yellowstone National Park.

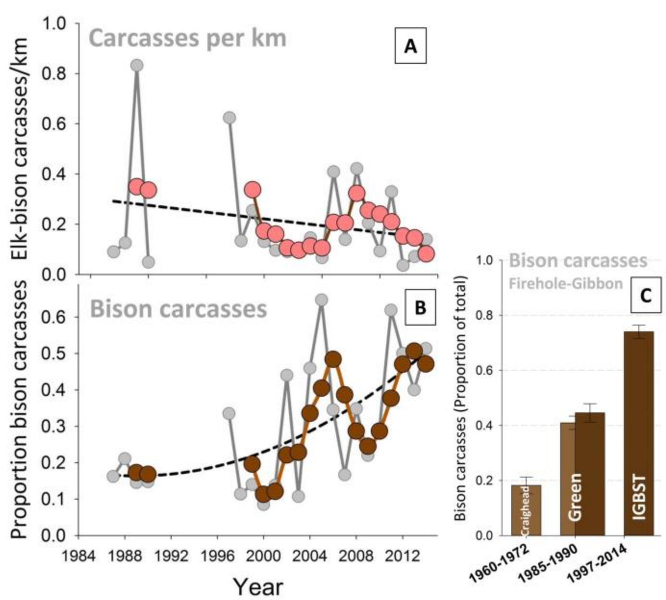


Figure 12. Trends in numbers of ungulate carcasses along transects surveyed during spring on winter ranges in Yellowstone National Park, 1985-2014 (A), as well as the proportion of those carcasses comprised of bison (B). Panel C shows proportional representation of bison carcasses for three studies spanning 55 years.

7. Annual Trends in Consumption of Meat by Bears

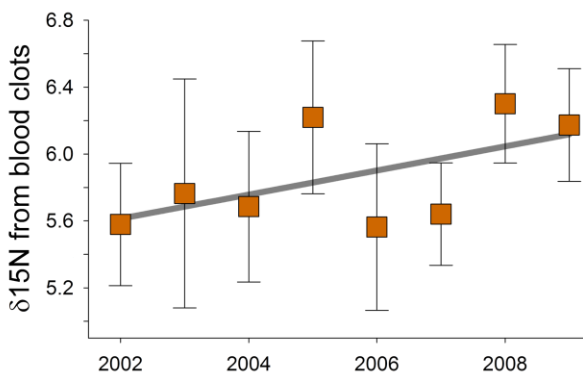


Figure 12. Trend in annual consumption of terrestrial meat as indicated by δ15N isotopes in blood obtained from grizzly bears captured in the Yellowstone ecosystem.

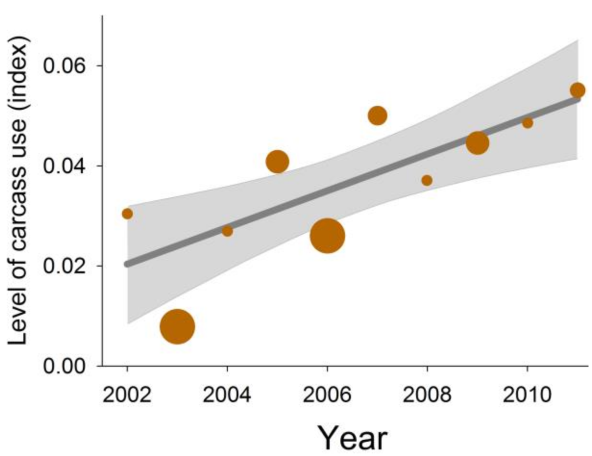


Figure 13. Trend in annual consumption of meat from ungulates as indicated by clusters of GPS locations obtained from radio-tracked Yellowstone grizzly bears. The size of data points is proportional to the size of whitebark pine cone crops estimated form observations along fixed transects, with larger dots corresponding with larger crops.

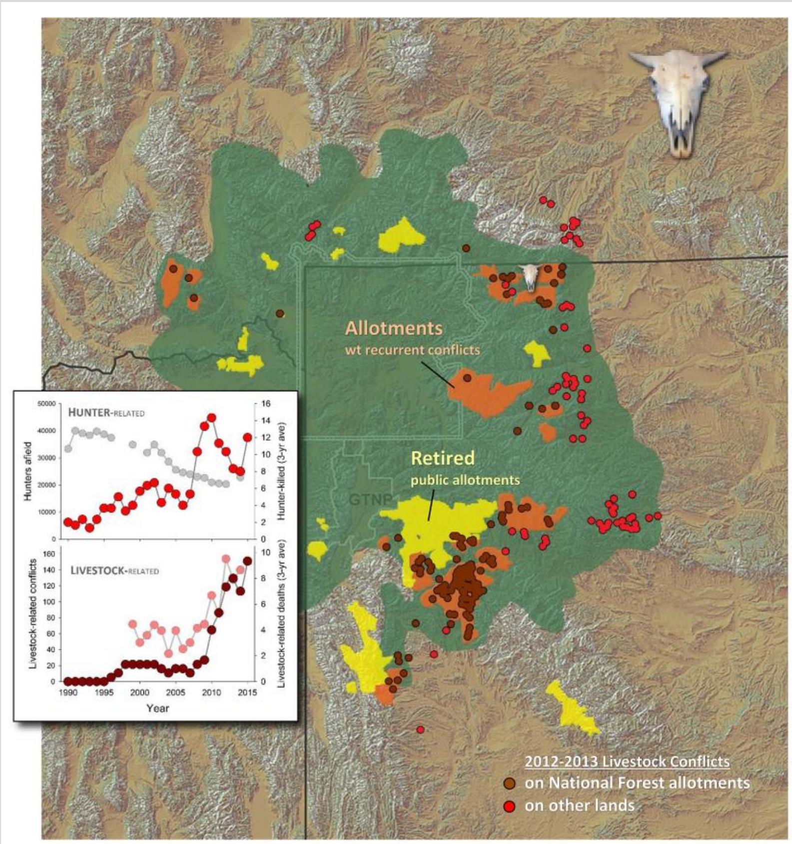
The Yellowstone ecosystem is highly dynamic, especially with the advent of major human-caused changes during the last 50 years. These changes most notably include climate change and the introduction of harmful non-native species, with dramatic impacts on key bear foods since especially the mid-1990s. Cutthroat trout (*Oncorhynchus clarkii*) have been essentially eliminated as a bear food by worsening hydrologic conditions and predation by non-native Lake trout (*Salvelinus namaycush*) [37,38]. Seeds from whitebark pine (*Pinus albicaulis*) have likewise been functionally eliminated in many places by an unprecedented outbreak of mountain pine beetles (*Dendroctonus ponderosae*) driven by a warming climate [39]. Longer-term, whitebark pine is likely to be further reduced by ever-increasing mortality caused by a non-native fungal disease called white pine blister rust (*Cronartium ribicola*) [40].

The compensatory response of Yellowstone's grizzly bears to loss of these two key foods has been well-documented [16,41,42]. They are eating increasing amounts of meat from terrestrial vertebrates—most notably ungulates such as bison, cattle (*Bos taurus*), and, perhaps, elk.

Figures 12 and 13, at left, document this trend. Isotopes in blood obtained from captured grizzly bears provides a window into how much meat they've been eating, specifically concentrations of isotopic Nitrogen [16]. Between 2002 and 2009 this isotopic concentration increased (Figure 12), indicative of increasing consumption of terrestrial meat coincident with maximum losses of whitebark pine to mountain pine beetles. Similarly, grizzly bears were more often exploiting ungulate carcasses [41], through at least 2012 (Figure 13). These latter data were obtained by documenting the behaviors of radio-marked grizzly bears, although researchers did not report which ungulate species were exploited—other than "large" versus "small."

All of this adds up to a conundrum. Yellowstone's grizzly bears have become increasingly reliant on meat from ungulates at precisely the same time that elk and moose populations were in major decline, along with one of two bison populations in the ecosystem. Without presenting all the circumstantial evidence, grizzly bears in this ecosystem were almost certainly eating more meat from livestock—especially cattle—on the periphery of the ecosystem (see Insert, below) [43], along with meat from bison nearer the core, most likely on the Northern Range.

8. Insert **Increasing Consumption of Meat from Livestock and Elk in Conflict with Humans**



There is little doubt that Yellowstone grizzly bears have turned to eating more meat under circumstances that bring them into conflict with humans, especially since 2007 in the wake of major losses of whitebark pine to bark beetles [39]. The map and figure to the left are illustrative of this trend. The top panel of the inset figure shows a 3-year-running average of grizzly bears killed by big-game hunters during surprise encounters or conflicts over hunter-killed elk (red dots). The bottom panel shows the same for grizzly bears killed because of conflicts over livestock (burgundy dots); actual numbers of livestock-related conflicts are shown by the pink data points. The gray trend line in the top panel shows numbers of elk hunters afield each year.

The map itself shows several overlays relevant to grizzly bear-livestock conflicts. The red and orange dots show the locations of conflicts during 2012-2013, the only years for which these data have been made publicly available in map form [43,44]. Areas in orange correspond with US Forest Service livestock grazing allotments that have had chronic conflicts since 2010; areas in yellow are allotments that have been closed (i.e., "retired") since 2000.

There are several implications. First, Yellowstone grizzly bears have been involved in mounting numbers of conflicts with humans over contested meat—principally livestock and actual or potential remains of hunter-killed elk. Numbers of bear mortalities consequently have sky-rocketed, especially since 2007. These increases have occurred, not because there are greater numbers of hunters or livestock in the ecosystem, but rather because grizzly bears are almost certainly eating more human-associated meat to compensate for losses of whitebark pine seeds, cutthroat trout, and free-ranging elk. Second, virtually all the livestock-related conflicts have occurred on the ecosystem periphery, in areas recently colonized by grizzlies. Most of this colonization occurred during the last 15-20 years, a period during which the population increased very little if at all [45].

The lethality of circumstances surrounding human-associated meat is in stark contrast to the much safer circumstances under which Yellowstone's grizzly bears have access to meat from bison.

9. Synopsis

Meat from ungulates is a high-quality bear food. Because of foraging efficiencies, this is especially true of meat available in large volumes from concentrated sources. Given these two axioms, meat from bison—the largest-bodied of any surviving Holocene ungulates—is predictably of great value to grizzly bears wherever they have access to this food. Because of European-perpetrated extirpations, this no longer occurs anywhere other than in the Yellowstone ecosystem—a 1% remnant of a system that occurred throughout most of the current western United States.

Data obtained during scientific investigations spanning nearly 60 years affirm not only the importance of meat to Yellowstone's grizzly bears, but more specifically the disproportionate importance of meat from bison carcasses. Grizzly bears here obtain a proportionally increasing amount of meat from bison, primarily from carcasses resulting from spring die-offs, complications of April-May birthing, and injuries sustained by bulls during the August-centered rut. Grizzly bears obtain more meat from bison carcasses and are more likely to exploit such a carcass compared to remains of elk, even accounting for the benefits derived from predation on smaller-bodied animals such as elk.

Recent research has conclusively shown that Yellowstone's grizzly bears are increasingly reliant on meat from ungulates because of declines in other important foods, notably cutthroat trout and whitebark pine. Substantial increases in conflicts over livestock and hunter-killed elk suggest that grizzlies are more often seeking meat under circumstances that bring them into conflict with humans—resulting in increasing levels of mortality for the involved bears. The one exception pertains to bison, specifically bison on Yellowstone National Park's Northern Range. Compelling circumstantial evidence suggests that grizzly bears in Yellowstone benefit from bison meat, not only for obtaining needed energy and nutrients, but, more importantly, obtained under circumstances that allow them to survive.

10. Literature Cited

[1] Mattson, D. J., & Merrill, T. (2002). Extirpations of grizzly bears in the contiguous United States, 1850–2000. Conservation Biology, 16(4), 1123-1136.

[2] Sanderson, E. W., Redford, K. H., Weber, B., Aune, K., Baldes, D., Berger, J., ... & Fearn, E. V. A. (2008). The ecological future of the North American bison: conceiving long-term, large-scale conservation of wildlife. Conservation Biology, 22(2), 252-266.

[3] https://www.allgrizzly.org/the-bison-factor

[4] https://www.allgrizzly.org/the-human-factor

[5] Mattson, D. J. (2017). Nutrition of ursids. Natural History of Grizzly Bears, 4, 1-19.

[6] Mattson, D. J. (1997). Use of ungulates by Yellowstone grizzly bears Ursus arctos. Biological Conservation, 81(1), 161-177.

[7] Mattson, D.J., Barber, K., Maw, R., & Renkin, R. (2004). Coefficients of productivity for Yellowstone's grizzly bear habitat. US Department of the Interior, US Geological Survey, Biological Science Report 2002-0007.

[8] https://www.allgrizzly.org/front-limbs

[9] https://www.allgrizzly.org/predation-on-ungulates

[10] Varley, N., & Gunther, K. A. (2002). Grizzly bear predation on a bison calf in Yellowstone National Park. Ursus, 13, 377-381.

[11] Wyman, T. (2002). Grizzly bear predation on a bull bison in Yellowstone National Park. Ursus, 13, 375-377.

[12] Carbyn, L. N., & Trottier, T. (1988). Descriptions of wolf attacks on bison calves in Wood Buffalo National Park. Arctic, 41(4), 297-302.

[13] Gunther, K. A., & Renkin, R. A. (1990). Grizzly bear predation on elk calves and other fauna of Yellowstone National Park. International Conference of Bear Research & Management, 8, 329-334.

[14] French, S. P., & French, M. G. (1990). Predatory behavior of grizzly bears feeding on elk calves in Yellowstone National Park, 1986-88. International Conference of Bear Research & Management, 8, 335-341.

[15] Jacoby, M. E., Hilderbrand, G. V., Servheen, C., Schwartz, C. C., Arthur, S. M., Hanley, T. A., ... & Michener, R. (1999). Trophic relations of brown and black bears in several western North American ecosystems. The Journal of Wildlife Management, 63(3), 921-929.

[16] Schwartz, C. C., Fortin, J. K., Teisberg, J. E., Haroldson, M. A., Servheen, C., Robbins, C. T., & Van Manen, F. T. (2014). Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. Journal of Wildlife Management, 78(1), 68-78.

[17] Hilderbrand, G. V., Schwartz, C. C., Robbins, C. T., Jacoby, M. E., Hanley, T. A., Arthur, S. M., & Servheen, C. (1999). The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology, 77(1), 132-138.

[18] Mowat, G., & Heard, D. C. (2006). Major components of grizzly bear diet across North America. Canadian Journal of Zoology, 84(3), 473-489.

[19] https://www.allgrizzly.org/terrestrial-meat

[20] Mattson, D. J. (2000). Causes and consequences of dietary differences among Yellowstone grizzly bears (*Ursus arctos*). Dissertation, University of Idaho, Moscow.

[21] Mattson, D. J., Blanchard, B. M., & Knight, R. R. (1991). Food habits of Yellowstone grizzly bears, 1977–1987. Canadian Journal of Zoology, 69(6), 1619-1629.

[22] Green, G. I., Mattson, D. J., & Peek, J. M. (1997). Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. The Journal of Wildlife Management, 61(40), 1040-1055.

[23] Green, G. 1994. Use of spring carrion by bears in Yellowstone National Park. M.S. Thesis, University of Idaho, Moscow.

[24] Gunther, K., & Wyman, T. (2016) Spring ungulate availability and use by grizzly bears in Yellowstone National Park. Pages 38-43 in van Manen, F. T., Haroldson, M. A., & Karabensh, B. E. (eds). Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2015. U.S. Geological Survey, Bozeman, Montana.

[25] Craighead, J.J., Sumner, J.S., & Mitchell, J.A. (1995). The grizzly bears of Yellowstone: Their ecology in the Yellowstone ecosystem, 1959-1992. Island Press, Washington, D.C.

[26] Garrott, R. A., White, P. J., & Rotella, J. J. (2008). The Madison headwaters elk herd: stability in an inherently variable environment. Pages 191-216 in Garrott, R. A., White, P. J., & Watson, F. G. R. (eds). The ecology of large mammals in central Yellowstone: sixteen years of integrated field studies. Elsevier.

[27] Hamlin, K. L., & Cunningham, J. A. (2009). Monitoring and assessment of wolf-ungulate interactions and population trends within the Greater Yellowstone Area, southwestern Montana, and Montana statewide: Final Report. Montana Department of Fish, Wildlife, and Parks, Wildlife Division, Helena, Montana, USA.

[28] Lubow, B. C., & Smith, B. L. (2004). Population dynamics of the Jackson elk herd. Journal of Wildlife management, 68(4), 810-829.

[29] Northern Yellowstone Cooperative Wildlife Working Group (2015). 2014-2015 Winter Count of Northern Yellowstone Elk. https://www.nps.gov/yell/learn/news/02042015.htm

[30] White, P. J., Wallen, R. L., & Hallac, D. E. (2015). Yellowstone bison: conserving an American icon in modern society. Yellowstone Association, Yellowstone National Park, Wyoming.

[31] MacNulty, D. R., Stahler, D. R., Wyman, C. T., Ruprecht, J., & Smith, D. W. (2016). The challenge of understanding northern Yellowstone elk dynamics after wolf reintroduction. Yellowstone Science, 24(1), 25-33.

[32] Wyoming Game & Fish Department, Annual Big Game Job Completion Reports. https://wgfd.wyo.gov/Hunting/Job-Completion-Reports

[33] Proffitt, K. M., Gude, J. A., Hamlin, K. L., Garrott, R. A., Cunningham, J. A., & Grigg, J. L. (2011). Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. Journal of Applied Ecology, 48(2), 471-478.

[34] Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Cook, J. G., Cook, R. C., Nelson, A. A., ... & Klaver, R. W. (2013). Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology, 94(6), 1245-1256.

[35] Brimeyer, D. G., & Thomas, T. P. (2004). History of moose management in Wyoming and recent trends in Jackson Hole. Alces, 40, 133-144.

[36] Tyers, D. B. (2006). Moose population history on the northern Yellowstone winter range. Alces, 42, 133-149.

[37] Kaeding, L. R. (2010). Relative contributions of climate variation, lake trout predation, and other factors to the decline of Yellowstone Lake cutthroat trout during the three recent decades. Dissertation, Montana State University, Bozeman.

[38] Gunther, K. A., Reinertson, E., Koel, T. M., Bigelow, P. E., & Ertel, B. (2016). Spawning cutthroat trout availability and use by grizzly bears in Yellowstone National Park. Pages 44-50 in van Manen, F. T., Haroldson, M. A., & Karabensh, B. E. (eds). Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2015. U.S. Geological Survey, Bozeman, Montana.

[39] Macfarlane, W. W., Logan, J. A., & Kern, W. R. (2013). An innovative aerial assessment of Greater Yellowstone Ecosystem mountain pine beetle-caused whitebark pine mortality. Ecological Applications, 23(2), 421-437.

[40] Hansen, A., Ireland, K., Legg, K., Keane, R., Barge, E., Jenkins, M., & Pillet, M. (2016). Complex challenges of maintaining whitebark pine in Greater Yellowstone under climate change: A call for innovative research, management, and policy approaches. Forests, 7(3), 54.

[41] Ebinger, M. R., Haroldson, M. A., van Manen, F. T., Costello, C. M., Bjornlie, D. D., Thompson, D. J., ... & White, P. J. (2016). Detecting grizzly bear use of ungulate carcasses using global positioning system telemetry and activity data. Oecologia, 181, 695-708.

[42] Orozco, K., & Miles, N. (2013). Use of diminished whitebark pine resources by adult female grizzly bears in Togwotee Pass, Spread Creek, and Mount Leidy in the Bridger-Teton National Forest, Wyoming, 2012. Pages 45-47 in van Manen, F. T., Haroldson, M. A., & West, K. (eds). Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2012. U.S. Geological Survey, Bozeman, Montana.

[43] Aber, B., Frey, K., Smith, J., DeBolt, B., Turnbull, Z., Boyce, M., Bales, K., & Gregory, Z. (2013). Grizzly bear-human conflicts in Idaho, Montana, and Wyoming. Pages 56-61 in van Manen, F. T., Haroldson, M. A., & West, K. (eds). Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2012. U.S. Geological Survey, Bozeman, Montana.

[44] Greater Yellowstone Area Grizzly Bear Habitat Modeling Team (2014). 2013 grizzly bear annual habitat monitoring report. Pages 78-96 in van Manen, F. T., Haroldson, M. A., West, K., & Soileau, S. C. (eds). Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2013. U.S. Geological Survey, Bozeman, Montana.

[45] http://www.grizzlytimes.org/single-post/2017/01/19/Fog-of-Science-II-Appling-and-Oranging-Grizzly-Bear-Numbers