

**MONITORING UNGULATE CARCASSES AND
GRIZZLY BEAR SCAVENGING ON THE NORTHERN
YELLOWSTONE WINTER RANGE**

By Heidi Engelhardt-Bergsjø, Daniel B. Tyers, Jon E. Swenson, Lynn R. Irby,
Jeremy P. Zimmer, Craig T. Olwert and Kasper Engelhardt-Bergsjø

INTERMOUNTAIN JOURNAL OF SCIENCES
Vol.15, No.1-3:7-17
September, 2009

MONITORING UNGULATE CARCASSES AND GRIZZLY BEAR SCAVENGING ON THE NORTHERN YELLOWSTONE WINTER RANGE

Heidi Engelhardt-Bergsjø¹, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway
Daniel B. Tyers, USDA Forest Service, Gardiner Ranger District, Box 5, Gardiner, MT 59030
Jon E. Swenson, Department of Ecology and Natural Resource Management, Norwegian University of Life Science, P.O. Box 5003, NO-1432 Ås, Norway and Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway
Lynn R. Irby, Professor emeritus, Montana State University, 1109 North Pinecrest, Bozeman, MT 59715
Jeremy P. Zimmer, USDA Forest Service, Gardiner Ranger District, Box 5, Gardiner, MT 59030
Craig T. Olwert, USDA Forest Service, Gardiner Ranger District, Box 5, Gardiner, MT 59030
Kasper Engelhardt-Bergsjø¹, USDA Forest Service, Gardiner Ranger District, Box 5, Gardiner, MT 59030

ABSTRACT

Ungulate carcasses are an important food source for scavengers, including grizzly bears (*Ursus arctos horribilis*), in the Greater Yellowstone Ecosystem. Each spring since 1989, nine transect routes in the Gardiner Basin, Montana, have been used to monitor availability of ungulate carcasses. We surveyed these transects during March-May 2006 and also conducted a complete search for carcasses on important parts of the Northern Yellowstone Winter Range (NYWR) adjacent to Yellowstone National Park (YNP). Our goals were to determine 1) how counts of ungulate carcasses on existing transects compared with more complete carcass counts along transects throughout the landscape and 2) document bear scavenging on the carcasses. Carcass density on existing transects was four times greater than on new transects, 0.8 vs. 0.2 carcasses/km, respectively. The original transects included areas where carcasses were most likely to be found and provided a good annual index of ungulate carcass availability. Starvation was the cause of death for 70 percent of recorded ungulates ($n = 106$). Contrary to findings inside YNP, we found very little evidence of grizzly bear predation or use of carcasses (1 of 106 carcasses) or total bear use (4 carcasses) in the Gardiner Basin. This may be due to a greater level of human disturbance or a lower density of bears on National Forest winter range compared to YNP winter range.

Key words: carcass, Gardiner Basin, grizzly bear, Northern Yellowstone Winter Range, scavenging, ungulates, *Ursus arctos horribilis*, winter mortality.

INTRODUCTION

To understand the dynamics of bears and ungulate populations, knowledge about predation and scavenging by bears is essential (Mattson 1997). Thus, it is important that management agencies consider ungulate carcass availability in their management strategies, including identification of human activities that influence access to carrion by bears, because human activities can influence spatial use by bears (Nellemann et al. 2007).

We envision a need for well-designed carcass surveys to monitor trends in carrion

availability, including areas outside YNP. Despite the recent removal of the grizzly bear from the Endangered Species List, its population status and availability of food sources still need to be monitored closely. Inside YNP the Interagency Grizzly Bear Study Team (IGBST) has monitored spring ungulate carcass availability on the YNP portion of the Northern Yellowstone Winter Range since 1986 (Cherry 2007). To supplement this monitoring, the Gardiner Ranger District, Gallatin National Forest (GNF), initiated 9 carcass transects in the Gardiner Basin north of YNP, on the lowest portion of the NYWR, in 1989. The first

¹ Nordre Soprim, 1970 Hemnes, Norway

goal of our study was to investigate whether these transects reflected carrion availability in the area.

A wide variety of organisms utilize carrion (DeVault et al. 2004). Facultative scavenging is a common strategy among vertebrates (Selva et al. 2005), and almost all vertebrate predators utilize carrion to some degree (DeVault et al. 2003). Recent investigations suggest that carrion use by vertebrates is a key ecological process (DeVault et al. 2003), and that carrion may account for a larger portion of the diet of some facultative scavengers than is now commonly assumed (DeVault and Rhodes 2002). Selva et al. (2005) suggested that scavenging by vertebrates is not a random process, but mediated by extrinsic factors and the scavengers' behavioral adaptations.

Selva et al. (2005) found that all 36 recorded scavenging species in their study in Poland (22 birds and 14 mammals) preferred predator-kills over animals that had died from other causes, and that almost all mammalian scavengers avoided non-ungulate carcasses. Many of the carnivorous species in the Greater Yellowstone Ecosystem (GYE), the area within and surrounding Yellowstone National Park (YNP) in the USA, rely on elk as their primary source of carrion (Gese et al. 1996). Coyotes (*Canis latrans*) are the most common scavenger on carcasses (Stahler et al. 2002, Weaver 1979). In addition, grizzly bears (*Ursus arctos horribilis*), black bears (*U. americanus*), and red foxes (*Vulpes vulpes*) utilize elk (*Cervus elaphus*) carrion available in the GYE as a result of predation or winter kill (Stahler et al. 2002).

The grizzly bear was listed as a "Threatened" species under the Endangered Species Act in the conterminous United States in 1975 (Glick 2005) and a recovery plan was prepared. All criteria set under the recovery plan were met and the GYE population was removed from the list of federally threatened species in March 2007 (Paige 2008).

Numerous ecological studies have been conducted on grizzly bears in the GYE. Studies of food habits have found substantial

seasonal and yearly variation in diet (Mattson et al. 1991, Mattson and Reinhart 1997, Mattson et al. 2002a, Mattson et al. 2002b, Mattson 2004, Mattson et al. 2005). Although grizzly bears are entirely vegetarian in some ecosystems (Rode et al. 2001), they will usually eat meat given the opportunity, and they can be effective scavengers and predators (Cole 1972, Mattson 1997).

Several studies have pointed out the importance of carcasses to grizzly bears (Mealey 1975, Green et al. 1997, Mattson 1997, Wilmers and Stahler 2002). Most scavenging occurs during spring and is associated with the abundance and relative availability of different types of carrion on ungulate winter ranges (Mattson 1997, Wilmers et al. 2003). Grizzly bears in the GYE use ungulates to a greater extent than most grizzly and brown bears in North America (Mattson et al. 1991), and they receive substantial energy from ungulates through predation and scavenging (Green et al. 1997, Mattson 1997). Robbins et al. (2006) estimated that 80 percent of the annual energy intake of adult males came from animal protein. Mattson (1997) estimated that 95 percent of the energy required by Yellowstone's grizzly bears during the non-denning season comes from elk, bison (*Bison bison*), and moose (*Alces alces*) and that 70 percent of ungulate meat in their diet came from scavenging. Our second goal was to document the level of bear scavenging activity in the area adjacent to YNP.

STUDY AREA

The study was conducted in the Gardiner Basin on the Gardiner Ranger District, GNF (45°2'13"N, 110°45'50"W), situated northeast of Gardiner in southwestern Montana, USA. The study area was part of the 1530-km² NYWR, where ungulates winter in large aggregations along the Yellowstone River (Houston 1982), and includes most of the range outside of YNP. The NYWR is described by Houston (1979). It falls within the GYE, one of the largest intact ecosystems in the

conterminous United States (USDA Forest Service 2008). The main streams running through the NYWR outside YNP are Palmer, Bear, Eagle, Phelps, Shaft House, Little Trail, Basset, Cedar, and Slip and Slide

creeks. The study area (Fig. 1) was restricted to USDA Forest Service and state lands east and north of the Yellowstone River historically used by wintering ungulates.

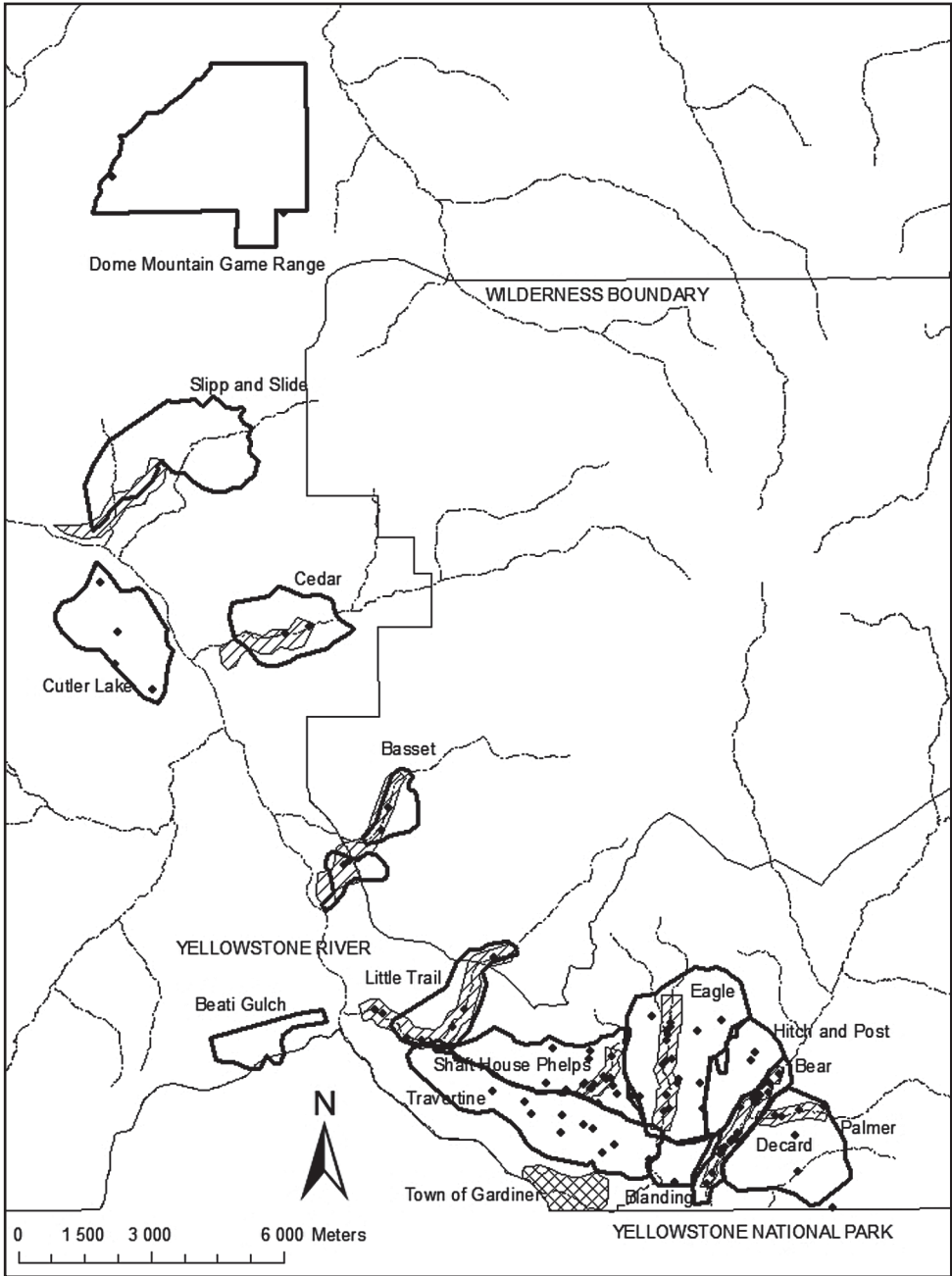


Figure 1. Map of the Gardiner Basin study area north of Yellowstone National Park showing boundaries of areas where landscape transects (solid thick lines) and original transects (polygons with stripes) were walked for the spring 2006 carcass survey. Black dots indicate carcass locations.

Elevation at the town of Gardiner, within the Gardiner Basin, is 1618 m. The average minimum temperature in Gardiner in January is -10 °C, and the average maximum temperature in July is 30 °C, annual average precipitation is 252 mm, and annual average snow fall is 635 mm. The highest amount of rainfall occurs in May and June (Western Regional Climate Center 2008). Precipitation increases and temperature decreases as elevation increases in the study area (Western Regional Climate Center 2008).

Vegetation in the Gardiner Basin consists primarily of big sagebrush (*Artemisia tridentata*) and grassland (dominated by blue-bunch wheatgrass, *Pseudoroegneria spicata*, and Idaho fescue, *Festuca idahoensis*) with scattered stands of Rocky Mountain juniper (*Juniperus scopulorum*) and limber pine (*Pinus flexilis*) at lower elevations, some quaking aspen (*Populus tremuloides*) at forest-grassland boundaries and in riparian areas, and Douglas-fir (*Pseudotsuga menziesii*) forests at mid-elevations. At higher elevations and on mid-elevation northern aspects, lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) are the dominant tree species.

METHODS

Each spring since 1989, nine transect routes have been examined in the Gardiner Basin to monitor the availability of ungulate carcasses for scavengers, usually by one person. Transects were generally oriented along waterways or followed existing trails along the major drainages in the Gardiner Basin. They were laid out by knowledgeable biologists to represent areas where wintering ungulates were presumed to congregate (and also, presumably, to die), and where bears were likely to forage on carrion. They were traveled on foot every 2 weeks from the first of March to the end of May. Ungulate mortality in YNP occurs mostly from March to May (Houston 1978, Schleyer 1983, Green et al. 1997, Mech et al. 2001).

We repeated these transects in 2006. One to three people walked the transects covering a linear distance of 23.0 km one or more times. Transects on which carcasses were recorded were re-run several times to record timing and extent of scavenging, resulting in a total distance examined of 64.2 km. Sampling intensity differed among drainages with more effort devoted to areas with higher carcass densities. These transects are hereafter referred to as *original transects*.

In addition to the original transects, we conducted an intensive search along a series of parallel lines, 200 m apart, that covered nearly all the ungulate winter range on public land within the study area to test the efficiency of the original survey technique. The systematic transect routes were oriented east–west or north–south, independently of drainage orientation. These additional transects included 126 lines across 15 major drainages (total length of 242.6 km). Green et al. (1997) indicated that, historically, carcass availability on the NYWR in YNP peaked the first half of April. This peak corresponded to the maximum accumulation of carcasses from starving animals before insects could reduce visibility of carcasses. Therefore, we conducted our searches between 15 April and 1 June. The systematic transects were sampled once, and are hereafter referred to as *landscape transects*.

For each carcass located on both types of transects, we recorded estimated time of death (winter or spring), species, sex, age, and cause of death. We also recorded site characteristics, including Universe Transverse Mercator (UTM) location, distance to forest edge, and cover. In addition, we described the site, and recorded if the carcass was visible from a road and whether or not the antlers had been removed from male ungulates and vestigial upper canine teeth (“ivories”) from both male and female elk carcasses. Both antlers and upper canines of elk have monetary value and a large number of recreational hikers seek these out each year. Removal of antlers and teeth provides some indication of the level of human use of the area, which could

be relevant in relation to grizzly bear use. We determined cause of death based on wounds on the carcass and evidence of predators, such as tracks, scats, or distinctive consumption patterns (Evans et al. 2006) and the condition of bone marrow in the metacarpus or metatarsus. Marrow fat is the last storage area of fat used by an animal in declining nutritional condition (Harris 1945). According to Harris (1945) signs of malnutrition are first evident in the tibia, and last in the metacarpus. If the bone marrow showed signs of starvation (red and jelly-like) (Greer 1968), the signs of predators were assumed to be from scavenging rather than predators. We made an effort to identify the appropriate scavenger(s). Scavenging rates were determined by repeated visits at the carcass sites on the original transects, and were approximate. We did not conduct any necropsy, except examination of the bone marrow. We were unable to calculate biomass consumed with our survey methodology.

To allow for an analysis of relative carcass densities among cover types related to cover type availability, we measured length of each cover type along each transect using Global Positioning System (GPS) and Geographic Information Systems (GIS) technology. Cover types were divided in to 21 categories (Table 1) following Yonge (2001). Because many cover types had too few carcasses for efficient analysis, cover types were combined into four vegetation groups: riparian, open vegetation, open forest, closed forest (Yonge 2001) (Table 1). This categorization was somewhat arbitrary, but it corresponded to vegetation structural features that have been demonstrated to be important for wildlife in the Yellowstone ecosystem (Mattson and Despain 1985).

Every time a change in cover type occurred along a transect (original or landscape), we marked the UTM coordinate at the point of the change. We used the GIS tool ET GeoWizards 9.6 (ET SpatialTechniques 2008) to create lines in Arc View (ESRI 2006) from the UTM coordinates. We calculated the distance traveled within each cover type using

Hawth's analysis tools (Beyer 2004). We compared the number of carcasses found/km of transect and the distributions of carcasses among cover types between the original and landscape transects.

We used the statistical package SPLUS (MathSoft Inc. S-Plus 2000) for statistical analyses. Differences in distribution of data sets among categorical variables, e.g., vegetation groups, were determined using Pearson's Chi-square or Fisher's exact tests when samples in individual cells were below acceptable numbers.

RESULTS

Data collection involved 74 full days in the field. We examined a total of 265.6 km of transects; 23.0 km of original transects (traveled multiple times, for a total of 64.2 km) and 242.6 km of landscape transects. We found 106 carcasses, 67 of mule deer (hereafter referred to as deer) and 39 of elk. We found 51 (30 deer and 21 elk) and 55 (37 deer and 18 elk) carcasses on the original and landscape transects, respectively. We found most (69) carcasses at Bear Creek, Eagle Creek, the Shaft House/Phelps Creek area, and Travertine Flats (Fig. 1).

The original transects had densities of carcasses that were about four times greater than the landscape transects ($\chi^2 = 45.35$, $P < 0.001$, 0.8 versus 0.2 carcasses/km, respectively). The pattern was similar for elk (0.33 versus 0.07 carcasses/km, $\chi^2 = 23.42$, $P < 0.001$) and deer (0.47 versus 0.15 carcasses/km, $\chi^2 = 21.42$, $P < 0.001$). Proportions of cover type groups differed between the two types of transect. The landscape transects had a lower proportion of total transect length in the riparian and closed forest groups and higher proportions of transects in the open sage/grass and open forest groups than original transects (χ^2 without Yate's correction: = 9.9257, $df = 3$, $P = 0.0192$; Table 1).

Contrary to our expectations, we found only four instances of bear scavenging activity, and determined only one to involve a grizzly bear (Table 2). In addition to one documented wolf kill, we found three additional elk in which wolf

Table 1. Segment lengths and carcasses located by cover classes (Mattson and Despain 1985, Yonge 2001) and groups (consolidation of classes into groups based on vegetation structure) on transects established in 1989 and walked annually to monitor carcasses in the Gardiner Basin (original transects) and transects covering the entire winter range outside Yellowstone National Park in the Gardiner Basin, Montana, walked only in 2006 (landscape transects). Data include only carcasses located in spring 2006.

Cover class/group	Landscape transects			Original transects		
	Segment length(m)	% of total transect	Carcasses	Segment length(m)	% of total transect	Carcasses
Riparian shrub	884		0	2,707		3
Cottonwood	678		1	55		0
Aspen	8,147		1	1,369		9
Riparian group	9,709	4%	2	4,131	18%	12
Sage/grass	188,814		42	5,971		6
Meadow	0		0	0		0
Tallus	3,973		2	30		0
Open vegetation group	192,787	80%	44	6,001	26%	6
Juniper-sage	3,466		2	530		3
Douglas fir - sage	4,491		2	0		0
Open conifer	15,544		1	780		0
Open aspen/conifer	509		1	195		2
Open forest group	24,010	10%	6	1,505	7%	5
Juniper	1,440		1	483		3
Juniper-DF 2 or 3 ¹	0			0		0
DF2	3,134			1,624		7
DF3	2,487		0	2,102		13
SF	254		0	1,159		1
DF-aspen	951		0	1,156		1
DF-cottonwood	385		0	1,720		1
LP3	3,521		0	0		0
DF3/riparian	229		0	1,454		1
DF	3,393		2	1,616		1
Aspen/SF	328			0		0
Closed forest group	16,122	7%	3	11,314	49%	28
Total transect length	242,628		55	22,951		51

¹DF = Douglas-fir, SF = spruce-fir, LP = lodgepole pine; 2= mature forest 100-300 years post disturbance, 3 = climax forest 300+ years post disturbance

predation was the probable cause of death. Of the 106 carcasses on both original and landscape transects, 70 percent were winterkills (Table 3).

Antlers and/or upper canines had been removed from 77 percent of male elk (including both transect sets). Antlers

had been removed from 33 percent of the antlered deer. No carcasses were visible from roads on the original transects. On the landscape transects 13 carcasses (7 deer and 5 elk) were visible from a road. Fifteen percent of the carcasses we found had not been fed on by mammalian scavengers.

Table 2. Carcasses that showed evidence of predation and/or scavenging when located on landscape and original transects in the Gardiner Basin, Montana, during spring 2006.

Scavenger/predator	Carcass species on:				
	Landscape transects		Original transects		All transects
	<i>Elk</i>	<i>Deer</i>	<i>Elk</i>	<i>Deer</i>	<i>Elk and Deer</i>
Mountain lion ¹	0	2	0	5	7
Bear	0	0	4	0	4
Wolf ¹	0	0	1	0	1
Canid (coyote or wolf)	13	19	10	12	54
Birds/maggots	1	0	2	4	7
Unknown	4	14	0	6	24
Not consumed	0	2	4	3	9
Total	18	37	21	30	106

¹Lions and wolves likely killed most or all carcasses attributed to them.

Table 3. Causes of death for elk and mule deer located on landscape and original transects in the Gardiner Basin, Montana, spring 2006. Cause of death was assigned based on patterns of carcass disturbance and bone marrow examination.

Cause of death	Landscape transects		Original transects		Total carcasses	
	<i>Elk</i>	<i>Deer</i>	<i>Elk</i>	<i>Deer</i>	<i>N</i>	<i>Percent</i>
Mountain Lion	0	2	0	5	7	6.6
Wolf	0	0	1	0	1	0.9
Unknown canid	1	0	0	0	1	0.9
Unknown predation	3	3	0	2	8	7.5
Hunter	0	1	0	0	1	0.9
Winterkill	12	25	17	20	74	69.8
Unknown	2	6	3	3	14	13.2
Total	18	37	21	30	106	100.0

DISCUSSION

Carcass Distribution on Landscape and Original Transects

The landscape transects, which mirrored vegetation cover group availability better than the original transects, had a lower proportion of total transect length in the riparian and closed forest cover classes and higher proportions of transects in the open vegetation and open forest cover classes than original transects. Both transect sets included segments in all of the major cover classes available on the NYWR. Relative density of carcasses was approximately four times greater on original transects than on landscape transects (0.8 vs. 0.2 carcasses/km, respectively). Because of the high proportion of open vegetation that provides for greater visibility of carcasses on the landscape transects, we assumed

that the number of carcasses we recorded on landscape transects was close to the true number available in spring 2006.

Overall, these data indicate that the original transects provided a reasonable (but not proportionate) coverage of available winter range habitat types and that they sampled areas where carcasses might more likely be found than on the winter range as a whole. Use of the original transect set should, therefore, provide a reasonable index of carcass availability among years rather than investing the large amount of time required to cover the entire winter range.

Scavenging Intensity

We found very little evidence of bear use of ungulate carcasses and only one documented grizzly bear scavenging event. As early as 1974, Houston (1978) conducted carcass counts on the NYWR inside YNP and standardized carcass counts have been

conducted inside YNP since 1986 (Cherry 2007). In 2006, 73 carcasses (elk and bison), or 0.49 carcasses/km, were found along 155.3 km of transects on the NYWR inside the park. Of these, 24 (33%) had been visited by bears (Podruzny and Gunther 2007). We found a carcass density of 0.2 and 0.8 carcasses/km on the landscape and original transects, respectively. Cherry (2007) argued that the only consistent index of carcass availability has been the number of carcasses/km and that no attempt has been made to estimate density. The routes in YNP were established based on knowledge about the likelihood of finding carcasses and where bears are known to forage in spring, not on a probability-based sampling method (Cherry 2007). This method has similarities to the sampling method we used on the original transects. Our data suggest that bear use of carcasses on the NYWR was much higher inside than outside YNP even though all of our study area was within grizzly bear distribution range (Schwartz et al. 2006).

There may be many reasons for the differences in carcass use. First, the level of human presence in spring is probably higher in the Gardiner Basin than inside YNP, as suggested by the large percentage of antlers removed from carcasses. Taking any naturally occurring object, including antlers, out of YNP is prohibited (USDI National Park Service 2008), so carcasses are more likely to be left undisturbed inside YNP. Mattson et al. (1987) found that the proportion of ungulate carcasses used by grizzly bears in YNP appeared to be influenced at a distance of 200–300 m from primary roads, and Green et al. (1997) determined that grizzly bear use of carcasses in YNP was lower within 400 m of a road and within 5 km of a major recreational development. Also, grizzly bear responses to roads depend on the type of human activity along the roads (Wielgus et al. 2002). In the Gallatin National Forest, public land is managed under a multiple use mandate and, as such, a wider variety of human activities are allowed and public use is much less restricted than in YNP (USDA Forest Service 1982). However, grizzly bears can

alter their diurnal behavioral pattern in response to human presence (Mueller et al. 2004). An alternate explanation for the lower scavenging rate by bears, particularly grizzly bears, on the NYWR outside YNP is lower bear density. This area is at the edge of the expanding grizzly bear distribution in the GYE (Schwartz et al. 2006). Bear population density tends to be low in the peripheral areas of expanding populations (Swenson et al. 1998). Many of the carcasses that had been fed on by mammals were only partially consumed and 15 percent had not been fed on by mammalian scavengers. Thus, the great abundance of carcasses in YNP might have satiated scavengers, so they did not require carrion outside the park, or total scavenger density may have been lower outside YNP, due to trapping and/or hunting or because some scavengers avoided areas where human-induced mortality might occur.

Our study was not designed to compare grizzly bear use of carcasses on these very differently managed landscapes, but such a study would be useful in understanding how grizzly bears deal with human presence and would be valuable for land managers charged with creating land-use regulations to minimize human impact on grizzly bear populations.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We conclude that the original transects initiated by the Gardiner Ranger District in 1989 provide a reasonable index to annual carcass abundance in the NYWR north of YNP. In areas where meat constitutes a major part of brown bears' diet, managers should take the availability and perpetuation of these resources into consideration (Hilderbrand et al. 1999). Variation in the availability of this important food source could affect the viability of populations of grizzly bears and other scavengers. The spatial and temporal distribution of carcasses must be addressed in management strategies, if the goal is conservation of specific wildlife populations or healthy ecosystems

(Hilderbrand et al. 1999). Thus, it is essential for managers to track long-term trends in the availability of carcasses. We, therefore, recommend continued monitoring of carcass distribution on the NYWR outside YNP using the original transects.

In spring 2006, 33 percent of the carcasses found on the NYWR in YNP had been visited by bears, compared with only 4 percent outside YNP. This may be due to grizzly bears responding to more ground-based human activities outside YNP, lower densities of bears outside YNP, or a combination of the two factors.

ACKNOWLEDGMENTS

We thank Stian Heid and Hans Ole Ørka for help with GIS analysis. We thank Gerry Bennett and Dick Ohman for financial support. Other support was provided by the Gardiner Ranger District, USFS.

LITERATURE CITED

- Beyer, H. L. 2004. Hawth's analysis tools for Arcgis. Available at <http://www.Spatialecology.Com/Htools>.
- Cherry, S. 2007. Monitoring ungulate carcasses and spawning cutthroat trout. P. 55 in C. C. Schwartz, M. A. Haraldson, and K. West, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2006. U.S. Geological Survey, Bozeman, MT.
- Cole, G. F. 1972. Grizzly bear elk relationships in Yellowstone National Park. *Journal of Wildlife Management* 36:556-561.
- DeVault, T. L., I. L. Brisbin, and O. E. Rhodes. 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. *Canadian Journal of Zoology* 82:502-509.
- DeVault, T. L. and O. E. Rhodes. 2002. Identification of vertebrate scavengers of small mammal carcasses in a forested landscape. *Acta Theriologica* 47:185-192.
- DeVault, T. L., O. E. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102:225-234.
- ESRI. 2006. Arc GIS Version 9.1. Environmental Systems Research Institute Inc., Redlands, CA.
- ET SpatialTechniques. 2008. ET Geowizards, Available at <http://Www.Ian-Ko.Com>
- Evans, S. B., L. D. Mech, P. J. White, and G. A. Sargeant. 2006. Survival of adult female elk in Yellowstone following wolf restoration. *Journal of Wildlife Management* 70:1372-1378.
- Gese, E. M., R. L. Ruff, and R. L. Crabtree. 1996. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. *Canadian Journal of Zoology* 74:769-783.
- Glick, D. 2005. Back from the brink. *Smithsonian* 36:54-62.
- Green, G. I., D. J. Mattson, and J. M. Peek. 1997. Spring feeding on ungulate carcasses by grizzly bears in Yellowstone National Park. *Journal of Wildlife Management* 61:1040-1055.
- Greer, K. R. 1968. A compression method indicates fat content of elk (wapiti) femur marrows. *Journal of Wildlife Management* 32:747-751.
- Harris, D. 1945. Symptoms of malnutrition in deer. *Journal of Wildlife Management* 9:319-322.
- Hilderbrand, G. V., S. G. Jenkins, C. C. Schwartz, T. A. Hanley, and C. T. Robbins. 1999. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology* 77:1623-1630.
- Houston, D. B. 1978. Elk as winter-spring food for carnivores in northern Yellowstone National Park. *Journal of Applied Ecology* 15:653-661.
- Houston, D. B. 1979. The northern Yellowstone elk - winter distribution and management. Pp. 263-272 in M. S.

- Boyce and L. J. Hayden, editors. North American elk: Ecology, behavior and Management, University of Wyoming, Laramie.
- Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publishing Co., New York, NY.
- MathSoft Inc. S-Plus. 2000. Data Analysis Products Division, Mathsoft. Seattle, WA.
- Mattson, D. J. 1997. Use of ungulates by Yellowstone grizzly bears - *Ursus arctos*. *Biological Conservation* 81:161-177.
- Mattson, D. J. 2004. Exploitation of pocket gophers and their food caches by grizzly bears. *Journal of Mammalogy* 85:731-742.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977-1987. *Canadian Journal of Zoology* 69:1619-1629.
- Mattson, D. J. and D. G. Despain. 1985. Grizzly bear habitat component mapping handbook for the Yellowstone Ecosystem. Forest Service, Yellowstone National Park, WY. 37 pp.
- Mattson, D. J., R. R. Knight, and B. M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear in Yellowstone National Park, Wyoming. *International Conference for Bear Research and Management* 7:259-273.
- Mattson, D. J., M. G. French, and S. P. French. 2002a. Consumption of earthworms by Yellowstone grizzly bears. *Ursus* 13:105-110.
- Mattson, D. J., S. R. Podrutzny, and M. A. Haroldson. 2002b. Consumption of fungal sporocarps by Yellowstone grizzly bears. *Ursus* 13:95-103.
- Mattson, D. J., S. R. Podrutzny, and M. A. Haroldson. 2005. Consumption of pondweed rhizomes by Yellowstone grizzly bears. *Ursus* 16:41-46.
- Mattson, D. J., and D. P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology* 34:926-940.
- Mealey, S. P. 1975. The natural food habits of free ranging grizzly bears in Yellowstone National Park 1973-1974. M.S. thesis, Montana State University, Bozeman.
- Mech, L. D., D. W. Smith, K. M. Murphy, and D. R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management* 65:998-1003.
- Mueller, C., Herrero, S., and M. L. Gibeau, 2004. Distribution of subadult grizzly bears in relation to human development in the Bow River Watershed, Alberta. *Ursus* 15:35-47.
- Nellemann, C., O.-G. Støen, J. Kindberg, J. E. Swenson, I. Vistnes, G. Ericsson, J. Katajisto, B. P. Kaltenborn, J. Martin, and A. Ordiz. 2007. Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. *Biological Conservation* 138:157-165.
- Paige, C. 2008. State of the grizzly. *Montana Outdoors, Magazine of Montana Fish, Wildlife and Parks*. March-April 2008. Available at <http://fwp.mt.gov/mtoutdoors/HTML/articles/2008/StateOfTheGrizzly.htm>
- Podrutzny, S. and K. Gunther. 2007. Spring ungulate availability and use by grizzly bears in Yellowstone National Park. In C.C. Schwartz, M.A. Haroldson, and K. West, editors. *Yellowstone Grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team*, 2006. U.S. Geological Survey, Bozeman, MT. p 19-20.
- Robbins, C. T., C. C. Schwartz, K. A. Gunther, and C. Servheen. 2006. Grizzly bear nutrition and ecology studies in Yellowstone National Park. The Interagency Grizzly Bear Study Team. *Yellowstone Science* 14:1-8 Available at <http://www.nrmcs.usgs.gov/files/norock/products/GrizzlyBearNutrition-Ecology>.
- Rode, K. D., C. T. Robbins, and L. A. Shipley. 2001. Constraints on herbivory by grizzly bears. *Oecologia* 128:62-71.

- Schleyer, B. O. 1983. Activity patterns of grizzly bears in the Yellowstone ecosystem and their reproductive behavior, predation and the use of carrion. M.S. thesis, Montana State University, Bozeman.
- Schwartz, C. C., M. A. Haroldson, K. A. Gunther, and D. Moody. 2006. Distribution of grizzly bears in the Greater Yellowstone Ecosystem in 2004. *Ursus* 17:63-66.
- Selva, N., B. Jedrzejewska, W. Jedrzejewski, and A. Wajrak. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology* 83:1590-1601.
- Stahler, D., B. Heinrich, and D. Smith. 2002. Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Animal Behaviour* 64:283-290.
- Swenson, J. E., F. Sandegren, and A. Söderberg. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *Journal of Animal Ecology* 67:819-826.
- USDA Forest Service. 1982. Gallatin National Forest, forest plans. Gallatin National Forest, Bozeman, MT. 180 pp.
- USDA Forest Service. 2008. Gallatin National Forest. Welcome to the Gallatin National Forest. Gallatin National Forest, Bozeman, MT. Available at <http://www.fs.fed.us/r1/gallatin/>
- USDI National Park Service. 2008. Yellowstone National Park, Available at <http://Home.Nps.Gov/Yell/Planyourvisit/Impact.Htm>.
- Weaver, J. L. 1979. Influence of elk carrion upon coyote populations in Jackson Hole, Wyoming. Pp. 152-157 in M.S. Boyce and L.J.Hayden, editors. *North American elk: ecology, behavior and management*, University of Wyoming, Laramie.
- Western Regional Climate Center. 2008. Montana climate summaries. National Oceanic and Atmospheric Administration, Accessed June 27, 2008. Available at <http://www.wrcc.dri.edu/summary/climsmmt.html>
- Wielgus, R. B., P. R. Vernier, and T. Schivatcheva. 2002. Grizzly bear use of open, closed, and restricted forestry roads. *Canadian Journal of Forest Research* 32:1597-1606.
- Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72:909-916.
- Wilmers, C. C. and D. R. Stahler. 2002. Constraints on active-consumption rates in gray wolves, coyotes, and grizzly bears. *Canadian Journal of Zoology* 80:1256-1261.
- Yonge, S. R. 2001. The ecology of grizzly bears and black bears in the Cooke City, Montana area. M.S. thesis, Montana State University, Bozeman. 88 pp.

Received 7 April 2009

Accepted 30 September 2009