

## Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park

Kerry A. Gunther<sup>1,3</sup> and Douglas W. Smith<sup>2,4</sup>

<sup>1</sup>*Bear Management Office, PO Box 168, Yellowstone National Park, WY 82190, USA*

<sup>2</sup>*Wolf Project, PO Box 168, Yellowstone National Park, WY, 82190, USA*

**Key words:** *Canis lupus*, cub mortality, grizzly bear, interference competition, interspecific killing, kleptoparasitism, *Ursus arctos*, wolf, Yellowstone National Park

*Ursus* 15(2):232–238 (2004)

Gray wolves (*Canis lupus*) were extirpated from Yellowstone National Park (YNP) by the 1920s through predator control actions (Murie 1940, Young and Goldman 1944, Weaver 1978), then reintroduced into the park from 1995 to 1996 to restore ecological integrity and adhere to legal mandates (Bangs and Fritts 1996, Phillips and Smith 1996, Smith et al. 2000). Prior to reintroduction, the potential effects of wolves on the region's threatened grizzly bear (*Ursus arctos*) population were evaluated (Servheen and Knight 1993). In areas where wolves and grizzly bears are sympatric, interspecific killing by both species occasionally occurs (Ballard 1980, 1982; Hayes and Baer 1992). Most agonistic interactions between wolves and grizzly bears involve defense of young or competition for carcasses (Murie 1944, 1981; Ballard 1982; Hornbeck and Horejsi 1986; Hayes and Mossop 1987; Kehoe 1995; McNulty et al. 2001). Servheen and Knight (1993) predicted that reintroduced wolves could reduce the frequency of winter-killed and disease-killed ungulates available for bears to scavenge, and that grizzly bears would occasionally usurp wolf-killed ungulate carcasses. Servheen and Knight (1993) hypothesized that interspecific killing and competition for carcasses would have little or no population level effect on either species.

As a component of post-reintroduction wolf and grizzly bear monitoring programs, interspecific interactions between the species were recorded. We expected reintroduced wolves to occasionally kill grizzly bears, especially cubs-of-the-year (cubs). We also predicted that

adult males, solitary adult females, and female grizzly bears accompanied by yearling or 2-year-old offspring would occasionally usurp wolf-killed ungulates and scavenge the remains. We hypothesized that these cohorts of grizzly bears would be more successful than subadults at usurping wolf-kills. We further hypothesized that due to potential danger to cubs, females with cubs would not attempt to displace wolf packs from their kills. Our monitoring of interspecific interactions between wolves and grizzly bears is ongoing. From wolf reintroduction in 1995 until January of 2003, 96 wolf-grizzly bear interactions have been recorded (Ballard et al. 2003; D. Smith, National Park Service, Yellowstone National Park, Wyoming, USA, unpublished data). Here we report observations of interactions between wolves and female grizzly bears with cubs and evidence of wolf packs killing grizzly bear cubs near carcasses. Due to grizzly bears' low reproductive rate (Schwartz et al. 2003) and status as a threatened species (USFWS 1993), the effects of wolves on carcass availability and cub survival is an important consideration for wolf reintroduction and grizzly bear conservation efforts.

YNP encompasses 891,000 ha in the states of Wyoming, Montana, and Idaho, USA. The park contains a variety of habitats from high elevation alpine to low elevation sagebrush grasslands (Despain 1990). YNP and the surrounding area (Greater Yellowstone Ecosystem, GYE) support an estimated 56,100 elk (*Cervus elaphus*), 29,500 mule deer (*Odocoileus hemionus*), 5,800 moose (*Alces alces*), 3,900 bighorn sheep (*Ovis canadensis*), 3,600 bison (*Bison bison*), and smaller numbers of whitetail deer (*Odocoileus virginianus*), mountain goat (*Oreamnos americanus*), and pronghorn antelope (*Antilocapra americana*) (U.S. Fish and Wildlife Service 1994). Large carnivores in the GYE include grizzly bears, American black bears (*U. americanus*), wolves, and mountain lions (*Felis concolor*). In 2002, the reintroduced wolf population in the GYE was estimated at 273 wolves in 31 packs (Smith et al. 2003a). More than 90% of the prey killed by wolves in the GYE is elk (Smith et al. 2003b). Other prey species killed by wolves include deer, bison, and moose, but individually none of these prey comprise >2% of GYE wolves' diet. The GYE grizzly bear population is estimated at 280–610 bears (Eberhardt and Knight 1996). The GYE is unique among areas inhabited by grizzly bears in North America because

<sup>3</sup>kerry\_gunther@nps.gov <sup>4</sup>doug\_smith@nps.gov



**Fig. 1.** An interaction between gray wolves and a female grizzly bear with 2 cubs-of-the-year in Pelican Valley, Yellowstone National Park, Wyoming, USA, 2000. The wolves are on the bank of the creek, which is 2–3 meters higher than the bears in the creek bottom. This makes the wolves appear larger in proportion to the bears than they were (photo by D. Smith).

of the substantial consumption of ungulate meat by bears (Mattson et al. 1991, Mattson 1997). Prior to wolf reintroduction, GYE grizzly bears obtained ungulate meat primarily by scavenging winter-killed elk and bison carcasses in spring (Green et al. 1997), by preying on elk calves in late spring and early summer (Gunther and Renkin 1990), and by preying on and scavenging rut-weakened and rut-killed elk and bison in late summer and fall (Mattson 1997).

### **Interactions between wolves and female grizzlies with cubs**

From 1995 through 2002, 96 wolf–grizzly interactions were recorded (Ballard et al. 2003, D. Smith, unpublished data). Only 8 (8%) of these interactions were between wolves and female grizzly bears with cubs (Fig. 1). Females with older offspring were also rarely

observed interacting with wolves. Only 7 (7%) interactions between wolves and females with yearlings or two-year olds were recorded.

Of the 8 interactions between wolves and female grizzly bears with cubs, 5 were at carcasses, 2 were at wolf rendezvous sites, and 1 occurred at a neutral site. In 3 of the 5 interactions at carcasses (Observations 1, 5, 8; Table 1), the bear family groups were displaced by wolves regardless of the number of wolves present (1–5 wolves). In 1 of these interactions (Observation 1; Table 1), a larger bear, probably a male, was feeding on the carcass before the female with cubs approached. After the lone bear left the carcass, a wolf fed on the carcass and the female with cubs left the area. The outcome of 1 interaction near a carcass was neutral (Observation 2; Table 1; Fig. 1). A female grizzly with 2 cubs encountered 4 adult wolves that were walking away from the carcass of a bull elk that was being controlled

**Table 1. Interactions between wolves and female grizzly bears with cubs in Yellowstone National Park, 1995–2002.**

| Observation | Date        | Bears                | Wolves                            | Location   | Dominant species     |
|-------------|-------------|----------------------|-----------------------------------|------------|----------------------|
| 1           | 6 Aug 1998  | Adult female, 1 cub  | 1 adult                           | Carcass    | Wolf                 |
| 2           | 12 Jul 2000 | Adult female, 2 cubs | 4 adult                           | Carcass    | Neutral <sup>a</sup> |
| 3           | 17 Jun 2001 | Adult female, 2 cubs | 4 adult, 2 yearlings              | Carcass    | Bear                 |
| 4           | 11 May 2002 | Adult female, 2 cubs | 1 adult, 1 yearling               | n/a        | Bear                 |
| 5           | 22 May 2002 | Adult female, 1 cub  | 1 adult, 2 yearlings              | Carcass    | Wolf                 |
| 6           | 31 Jul 2002 | Adult female, 3 cubs | 5 adult, 3 pups                   | Rendezvous | Wolf                 |
| 7           | 8 Aug 2002  | Adult female, 3 cubs | 3 pups                            | Rendezvous | Neutral              |
| 8           | 21 Sep 2002 | Adult female, 1 cub  | 2 adult, 1 yearling,<br>2 unknown | Carcass    | Wolf                 |

<sup>a</sup>Lone adult bear had possession of bull elk carcass, female with 2 cubs walking toward the carcass interacted with 4 wolves leaving the carcass.

by a single grizzly bear. After a brief standoff, the wolves continued walking away from the carcass and the female with cubs continued walking toward the carcass. Although the interaction with the wolves was neutral, the female with cubs did not attempt to usurp the carcass from the single adult bear.

In the other interaction at a carcass (Observation 3, Table 1), a female with 2 cubs successfully usurped a carcass from 6 wolves. On 17 June 2001 at 0606 hours, 6 members of the Druid Peak pack were observed in Lamar Valley feeding on the carcass of a cow elk they had probably killed the previous night. The 6 pack members present included radiomarked wolves 21 (the alpha male) and adults 106F, 217F, and 224M, as well as two unmarked yearlings. The remaining 20 adult and yearling wolves of the pack were not at the carcass, nor were the 11 pups from two litters. At 0614 hours, an adult female grizzly bear with 2 cubs was observed approaching the carcass from the west. When the bears neared the carcass, the wolves circled and confronted them. As the bears faced wolves that were directly in front of them, other wolves rushed in and bit at the bears from behind. The cubs stayed directly beside or beneath their mother as she slowly continued toward the carcass. Periodically, the female stopped to protect herself and lunged and swatted at the wolves. At times all 3 bears lunged together at an approaching wolf; other times the adult or cubs lunged independently at approaching wolves.

Several times the wolves completely stopped the bears' progress toward the carcass as the bears whirled around to face the circling wolves. The bears took approximately 20 minutes to move the final 100 meters to the carcass. At 0646 hours the bears reached the kill and began to scavenge. The wolves continued to circle the scavenging bears, but only occasionally rushed and

harassed them. At 0734 hours, after feeding on the carcass for about 48 minutes, the bears left the kill and walked away to the southwest. The wolves did not harass the bears as they left. None of the bears was hurt.

Two encounters between wolves and female grizzly bears with cubs were observed at wolf rendezvous sites. In late July 2002 (Observation 6, Table 1), 5 adult wolves and 3 wolf pups were at their rendezvous site when a female grizzly with 3 cubs walked through the site. One wolf approached the bears and followed them out of the area and no further interactions ensued. One week (Observation 7, Table 1) later, the same 4 bears walked through the same wolf rendezvous site when only the 3 wolf pups were present. The pups fled the area upon sighting the bears; the bears left the area with no visible response to the pups.

One other interaction between wolves and a female grizzly bear with cubs did not involve a carcass or rendezvous site (Observation 4, Table 1). A female with 2 cubs was walking within 1 km of a wolf den site when 2 wolves approached her. The adult bear charged at the wolves. The wolves stopped their approach and retreated but did not leave the area. The female and cubs left the area, and no other interaction was recorded.

### Interspecific killing of grizzly cubs by wolves

Although the interactions were not observed, we documented 2 incidents in which wolf packs likely killed grizzly bear cubs. The first incident occurred in late June or early July. On 2 July 2001, we received a report of a dead grizzly bear cub near Alum Creek in Hayden Valley. We hiked to the site 2 days later and retrieved the carcass of a male grizzly bear cub that we

**Table 2. Center-to-center, width measurements (mm) of upper and lower canines from reference skulls of grizzly bears, black bears, gray wolves, and mountain lions in the Greater Yellowstone Ecosystem.**

| Species       | Canine width | Mean (mm) | SD (mm) | Range (mm) | Number |
|---------------|--------------|-----------|---------|------------|--------|
| Grizzly bear  | Upper        | 58        | 5       | 48–69      | 35     |
|               | Lower        | 53        | 6       | 35–66      | 35     |
| Black bear    | Upper        | 50        | 4       | 43–60      | 31     |
|               | Lower        | 45        | 4       | 37–55      | 31     |
| Gray wolf     | Upper        | 45        | 3       | 40–53      | 33     |
|               | Lower        | 40        | 3       | 35–47      | 33     |
| Mountain lion | Upper        | 40        | 4       | 29–49      | 62     |
|               | Lower        | 35        | 4       | 23–41      | 62     |

estimated had been dead for 3 to 5 days. The carcass had been picked at by small avian scavengers but was less than 5% consumed. Field inspection of the carcass revealed that the dead cub had canine puncture wounds to the body and head as well as a crushed skull, indicating infliction by a large predator. The nearest climbable escape tree was 111 meters away. The nearest contiguous forest large enough to provide escape or hiding cover was 397 meters away. Fresh grizzly bear and wolf tracks were observed nearby, but were probably left after the cub had been killed (based on recent heavy rains). A bull elk carcass that was >90% consumed was found approximately 50 meters southeast of the dead cub. The hide of the elk carcass was inverted, suggesting scavenging by bears; however, the cause of death was unknown.

A laboratory necropsy was performed on the cub carcass to determine the species of predator that killed it. The cub was in average physiologic condition prior to death. Examination of the carcass revealed numerous puncture wounds to the head, chest, and abdomen. The parietal and temporal portions of the skull were crushed, several ribs were broken, and the abdominal region showed trauma. The distance between the centers of matching canine puncture wounds was measured from the hide. Distances between puncture wounds ranged from 38 to 42 mm.

The second incident occurred at the carcass of a bull bison that died in Lamar Valley on 3 August. Prior to death, the bison was observed with a wound on its side likely caused by another bull during the rut. Grizzly bears were first observed feeding on the carcass on the morning of 7 August. A female grizzly bear with 2 cubs as well as a single adult grizzly bear were observed scavenging the bison carcass on the night of 10 August. On 11 August at 0543 hours, 10 members of the Druid

Peak wolf pack were observed sniffing, chewing on, and playing with the carcass of a grizzly bear cub near the bull bison carcass. We investigated the site and retrieved the carcass of a female grizzly bear cub. The cub had multiple canine puncture wounds to its body but was <5% consumed. Field inspection of the carcass indicated that the wounds were consistent with attack by a large predator. Circumstantial evidence suggested that the cub had likely been killed by either the Druid Peak pack or the single adult grizzly bear observed at the bison carcass the previous night. The Druid Peak pack consisted of 6 adults, 20 yearlings, and two litters totaling 11 pups, for a total of 37 pack members (Smith and McIntyre 2002). The pups had not yet left the den sites and had not been observed at the bison carcass. The nearest climbable escape tree was 336 meters away. The nearest contiguous forest large enough to provide escape or hiding cover was 1,193 meters away.

The cub carcass was retrieved for laboratory necropsy to determine the species of predator that killed it. The cub weighed 22.7 kg, was in fair to good postmortem condition, and prior to death had been in good physiologic condition with no evidence of disease. Bite marks were observed over the majority of the body. Center-to-center distance between matching canine puncture wounds associated with hemorrhage and traumatized tissue (indicating occurrence while the cub was still alive) measured 33–44 mm, most >39 mm.

Although no one observed either incident, available evidence from the carcasses suggests that wolves killed both cubs. The distances between canine puncture wounds were 38–42 mm and 33–44 mm on the cubs killed in Hayden and Lamar Valleys, respectively, consistent with the center-to-center distances between canines of wolves, mountain lions, and small black bears from the GYE (Table 2). Canine widths in those ranges are too small to have been inflicted by grizzly bears (Table 2).

Predation by mountain lions is not likely in either incident. In YNP, mountain lions typically inhabit Douglas-fir (*Pseudotsuga menziesii*) and spruce (*Picea engelmannii*)-fir (*Abies lasiocarpa*) forest types containing numerous rocky canyons and outcrops (T. Ruth, Hornocker Wildlife Institute, Gardiner, Montana, USA, personal communication, 2001). Both kill sites were in large, nearly treeless sagebrush grasslands, not typical of mountain lion habitat in the GYE (Murphy et al. 1999), and lions are rarely observed in the non-forested portions of either Hayden or Lamar Valleys (T. Ruth, personnel communication, 2001). Both cubs were killed near the carcasses of large ungulates that had attracted grizzly bears and wolves. The presence of grizzly bears

and wolves would likely have precluded scavenging by mountain lions, which are smaller than bears and, as solitary animals, are vulnerable to wolf packs (Murphy et al. 1998). These physical and behavioral characteristics would have made it difficult for mountain lions to defend themselves against grizzly bears and wolves at carcasses located so far from escape trees.

Predation by black bears is not likely either. Both grizzly cubs were killed in large, non-forested areas far from forest cover. In YNP, black bears are rarely observed far from forest cover in large non-forested areas (Gunther et al. 1995). Due to their smaller body size, black bears are at a competitive disadvantage with grizzly bears in large non-forested areas (Herrero 1979). Black bears are generally subordinate to (Barnes and Bray 1967) and are sometimes killed by grizzly bears (Arnold 1930, Mattson et al. 1992, Gunther et al. 2002). It is unlikely that black bears would attempt to kill grizzly bear cubs, which are usually accompanied and aggressively defended by their mothers. It is also unlikely that black bears would compete with wolf packs and grizzly bears at ungulate carcasses located so far from escape trees or forest cover.

Elk, the primary prey of wolves in the GYE, are abundant in Hayden and Lamar Valleys, which are occupied by the Nez Perce and Druid Peak wolf packs, respectively (Smith et al. 2003b). In addition, the range in distances between canine puncture wounds in the hides of both cubs suggests that they were attacked by more than one animal, consistent with predation by wolves that typically live, travel, and hunt in packs (Mech 1970, Paradiso and Nowak 1982), but not by solitary mountain lions (Dixon 1982) or black bears (Jonkel 1978, Pelton 1982).

We used the center-to-center distance of matching canine puncture wounds in the hides of the dead cubs to aid in determining the species of predator that killed them. Use of canine puncture wound width measurements is an imperfect science. Multiple bites to flexible skin capable of stretching or shrinking make such measurements imprecise. In addition to canine puncture wound width measurements, we used vegetation cover type, landscape physiographic features, and social behavior of local predators to aid in identifying the species that likely killed the cubs. Although we cannot completely rule out predation by a mountain lion or small black bear in either incident, the preponderance of evidence suggests that wolves killed both grizzly cubs.

## Discussion

Female grizzly bears with cubs were successful at usurping carcasses from wolves in only 1 of 5 observed interactions at carcasses. Wolves displaced the female grizzly bears with cubs in 3 interactions observed at carcasses; in 1 incident the outcome was neutral for a carcass in the possession of a large adult grizzly bear that displaced both wolves and a female bear with cubs. Although we documented 1 case of a female grizzly bear with cubs usurping a carcass, interactions between wolves and grizzly bears with dependent young were rare during our study. Avoidance of wolves by female grizzlies with cubs is likely advantageous, as we documented 2 cubs that were probably killed by wolves.

Our documentation of an adult female grizzly bear with 2 cubs successfully usurping an elk carcass from 6 members of the Druid Peak pack is contrary to our hypothesis that due to potential danger to cubs, females with cubs would not attempt to displace wolf packs from kills. In this incident, the wolves had been feeding on the elk carcass before the female grizzly bear with cubs arrived and may have already been gorged and satiated. Wolves with full stomachs may give up carcasses more readily than hungry wolves. In addition, only 6 of the 26 pack members (not counting pups) were present, likely contributing to the bear family group's success in usurping the carcass. Although the energy gained by female grizzly bears with dependent cubs that usurp wolf-killed ungulates is potentially significant, there are also risks associated with kleptoparasitism, as demonstrated by the 2 cubs killed by wolf packs near ungulate carcasses.

Our documentation of 2 incidents of probable killing of grizzly bear cubs by wolf packs is consistent with our prediction that interspecific killing would occur following reintroduction of wolves to the GYE. Both incidents occurred near carcasses of large ungulates that attracted the bears and wolves. In both incidents it appeared that the cubs were attacked and bitten by more than one wolf, which is consistent with wolf-wolf intraspecific killing. The wolves did not consume the cubs in either incident. In the 8 years (1995–2002) since implementation of the GYE wolf reintroduction program, these are the first incidents documented in the GYE of interspecific killing of grizzly bear cubs by wolves. The 2 grizzly bear cubs killed by wolves in 2001 represent 3% of the 78 grizzly cubs (Haroldson 2002) counted that year and <1% of the 556 cubs (Haroldson 2002) counted in the GYE for the 8-year period following wolf reintroduction. However, because grizzly bear cubs in the GYE are not radiomarked (M.A. Haroldson et al.

Interagency Grizzly Bear Study Team, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana, USA, unpublished data), not all cub mortality is detected.

These observations lend insight into interference competition between wolves and grizzly bears and factors that contribute to interspecific killing of grizzly bear cubs by wolves. Further monitoring of wolf-grizzly bear interactions may expand our knowledge of the relative energy gained by adult female grizzly bears that usurp wolf-killed ungulates, in relation to the costs in terms of increased cub mortality associated with kleptoparasitism.

### Acknowledgments

We thank R. McIntyre, D. Stahler, K. Murphy, D. Guernsey, and R. Stradley for assistance collecting data on wolf-grizzly bear interactions. D. Ireland, T. Wyman, and S. Chin helped retrieve wolf-killed cub carcasses and helped investigate the kill sites. N. Anderson conducted laboratory necropsy of the cubs. N. Varley and R. McIntyre provided accounts of the incident they witnessed in which a female grizzly bear with cubs usurped a wolf-killed elk carcass. T. Ruth provided canine width measurements from GYE mountain lions. D. Ireland and T. Schock assisted with measurements of canine widths from reference skulls. We thank D. Boyd and an anonymous reviewer as well as Editor R. Harris and Technical Editor M. Munson-McGee for comments that improved this manuscript. R. Gray provided helpful editorial comments. The Yellowstone Center for Resources provided support for wolf and grizzly bear research and monitoring programs in YNP.

### Literature cited

- ARNOLD, B. 1930. Cannibal bear. *Yellowstone Nature Notes* 7(8):54.
- BALLARD, W.B. 1980. Brown bear kills gray wolf. *Canadian Field-Naturalist* 94:91.
- . 1982. Gray wolf-brown bear relationships in the Nelchina Basin of south-central Alaska. Pages 71–80 in F.H. Harrington and P.C. Paquet, editors. *Wolves of the world*. Noyes Publications, Park Ridge, New Jersey, USA.
- , L.N. CARBYN, AND D.W. SMITH. 2003. Wolf interactions with non-prey. Pages 259–271 in L.S. Mech and L. Boitani, editors. *Wolves: ecology, behavior, and conservation*. The University of Chicago Press, Chicago, Illinois, USA.
- BANGS, E.E., AND S.H. FRITTS. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin* 24:402–413.
- BARNES, V.G., AND O.E. BRAY. 1967. Population characteristics and activities of black bears in Yellowstone National Park. Final Report, Colorado Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, USA.
- DESPAIN, D.G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart, Boulder, Colorado, USA.
- DIXON, K.R. 1982. Mountain lion. Pages 711–727 in J.A. Chapman and G.A. Feldhamer, editors. *Wild mammals of North America: Biology, management, and economics*. John Hopkins University Press, Baltimore, Maryland, USA.
- EBERHARDT, L.L., AND R.R. KNIGHT. 1996. How many grizzlies in Yellowstone? *Journal of Wildlife Management* 60: 416–421.
- 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.
- GUNTHER, K.A., AND R.A. RENKIN. 1990. Grizzly bear predation on elk calves and other fauna of Yellowstone National Park. *International Conference on Bear Research and Management* 8:329–334.
- , M.J. BIEL, K.A. CHURCHILL, AND R.L. DANFORTH. 1995. Changing problems in Yellowstone bear management, 23 years after the dumps. Pages 85–110 in A.P. Curlee, A.M. Gillesberg, and D. Casey, editors. *Greater Yellowstone predators, ecology and conservation in a changing landscape*. Proceedings of the Third Biennial Conference on the Greater Yellowstone Ecosystem. Northern Rockies Conservation Cooperative, Jackson, Wyoming, and Yellowstone National Park, Mammoth, Wyoming, USA.
- , ———, N. ANDERSON, AND L. WAITS. 2002. Probable grizzly bear predation on an American black bear in Yellowstone National Park. *Ursus* 13:372–374.
- HAROLDSON, M.A. 2002. Unduplicated females. Pages 12–16 in C.C. Schwartz and M.A. Haroldson, editors. *Yellowstone grizzly bear investigations: Annual report of the Interagency Grizzly Bear Study Team, 2001*. U.S. Geologic Survey, Bozeman, Montana, USA.
- HAYES, R.D., AND D.H. MOSSOP. 1987. Interactions of wolves, *Canis lupus*, and brown bears, *Ursus arctos*, at a wolf den in the Northern Yukon (Canada). *Canadian Field-Naturalist* 101:603–604.
- , AND A. BAER. 1992. Brown bear, *Ursus arctos*, preying upon gray wolf, *Canis lupus*, pack. *Canadian Field-Naturalist* 107:373–374.
- HERRERO, S. 1979. Black bears: the grizzly's replacement? Pages 179–195 in D. Burke, editor. *The black bear in modern North America*. Boone & Crockett Club. The Amwell Press, Clinton, New Jersey, USA.

- HORNBECK, G.E., AND B.L. HOREJSI. 1986. Grizzly bear, *Ursus arctos*, usurps wolf, *Canis lupus*, kill. *Canadian Field-Naturalist* 100(2):259–260.
- JONKEL, C. 1978. Black, brown (grizzly), and polar bears. Pages 227–248 in J.L. Schmidt and D.L. Gilbert, editors. *Big game of North America, ecology, and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- KEHOE, N.M. 1995. Grizzly bear, *Ursus arctos*, wolf, *Canis lupus*, interaction in Glacier National Park, Montana. *The Canadian Field-Naturalist* 109(1):117–118.
- MATTSON, D.J. 1997. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biological Conservation* 81:161–177.
- , B.M. BLANCHARD, AND R.R. KNIGHT. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* 69:1619–1629.
- , R.R. KNIGHT, AND B.M. BLANCHARD. 1992. Cannibalism and predation on black bears by grizzly bears in the Yellowstone Ecosystem, 1975–1990. *Journal of Mammalogy* 73:422–425.
- McNULTY, D.R., N. VARLEY, AND D.W. SMITH. 2001. Grizzly bear, *Ursus arctos*, usurps bison calf, *Bison bison*, captured by wolves, *Canis lupus*, in Yellowstone National Park, Wyoming. *Canadian Field-Naturalist* 115(3):495–498.
- MECH, L.D. 1970. The wolf: the ecology and behavior of an endangered species. *The American Museum of Natural History*. The Natural History Press, Garden City, New York, USA.
- MURIE, A. 1940. Ecology of the coyote in the Yellowstone. *Fauna of the National Parks, Fauna Series 4*. U.S. Government Printing Office, Washington, D.C., USA.
- . 1944. *The wolves of Mount McKinley*. U.S. Department of the Interior, National Park Service, *Fauna of the National Parks of the United States, Faunal Series 5*. U.S. Government Printing Office, Washington, D.C., USA.
- . 1981. *The grizzlies of Mount McKinley*. U.S. Department of the Interior, National Park Service, *Scientific Monograph Series No. 14*. U.S. Government Printing Office, Washington, D.C., USA.
- MURPHY, K.M., G.S. FELZIEN, M.G. HORNOCKER, AND T.K. RUTH. 1998. Encounter competition between bears and cougars: Some ecological implications. *Ursus* 10:55–60.
- , P. IAN ROSS, AND M.G. HORNOCKER. 1999. The ecology of anthropogenic influences on cougars. Pages 77–101 in A. Peyton Curlee, S.C. Minta, and P.M. Kareiva, editors. *Carnivores in ecosystems: The Yellowstone experience*. Yale University Press, New Haven, Connecticut, USA.
- PARADISO, J.L., AND R.M. NOWAK. 1982. Wolves. Pages 460–474 in J.A. Chapman and G.A. Feldhamer, editors. *Wild mammals of North America: Biology, management, and economics*. John Hopkins University Press, Baltimore, Maryland, USA.
- PELTON, M.R. 1982. Black bear. Pages 504–514 in J.A. Chapman and G.A. Feldhamer, editors. *Wild mammals of North America: Biology, management, and economics*. John Hopkins University Press, Baltimore, Maryland, USA.
- PHILLIPS, M.P., AND D.W. SMITH. 1996. *The wolves of Yellowstone*. Voyageur Press, Stillwater, Minnesota, USA.
- SCHWARTZ, C.C., S.D. MILLER, AND M.A. HAROLDSON. 2003. Grizzly bear. Pages 556–586 in G.A. Feldhammer, B.C. Thompson, and J.A. Chapman, editors. *Wild Mammals of North America: Biology, management, and conservation*. Second edition. The John Hopkins University Press, Baltimore, Maryland, USA.
- SERVHEEN, C., AND R.R. KNIGHT. 1993. Possible effects of a restored gray wolf population on grizzly bears in the Greater Yellowstone Area. Pages 28–37 in R.S. Cook, editor. *Ecological issues on reintroducing wolves into Yellowstone National Park*. Scientific Monograph NPS/NRYELL/NRSM-93/22. U.S. Department of the Interior, National Park Service, Natural Resources Publication Office, Denver, Colorado, USA.
- SMITH, D.W., AND R. MCINTYRE. 2002. Wolf pack size: How did the Druid Peak pack get to be so big? *International Wolf* 12(1):4–7.
- , L.D. MECH, M. MEAGHER, W.E. CLARK, R. JAFFE, M.K. PHILLIPS, AND J.A. MACK. 2000. Wolf–bison interactions in Yellowstone National Park. *Journal of Mammalogy*, 81:1128–1135.
- , D.R. STAHLER, AND D.S. GUERNSEY. 2003a. *Yellowstone Wolf Project: Annual Report, 2002*. YCR-NR-2003. National Park Service, Yellowstone National Park, Wyoming, USA.
- , R.O. PETERSON, AND D.B. HOUSTON. 2003b. *Yellowstone after wolves*. *BioScience* 53:330–340.
- U.S. FISH AND WILDLIFE SERVICE. 1993. *Grizzly bear recovery plan*. Missoula, Montana, USA.
- . 1994. *The reintroduction of gray wolves to Yellowstone National Park and central Idaho*. Final Environmental Impact Statement. Helena, Montana, USA.
- WEAVER, J. 1978. *The wolves of Yellowstone*. Natural Resources Report 14. U.S. Department of Interior, National Park Service, Washington D.C., USA.
- YOUNG, S.P., AND E.A. GOLDMAN. 1944. *The wolves of North America*. Dover Publications, New York, New York, USA.

Received: 9 January 2004

Accepted: 1 March 2004

Associate Editor: R.B. Harris