Grizzly bear–human conflicts in the Greater Yellowstone ecosystem, 1992–2000

Kerry A. Gunther[1,6], Mark A. Haroldson[2,7], Kevin Frey[3,8], Steven L. Cain[4,9], Jeff Copeland[5,10], and Charles C. Schwartz[2,11]

[1]*Bear Management Office, PO Box 168, Yellowstone National Park, WY 82190, USA*
[2]*Interagency Grizzly Bear Study Team, Northern Rocky Mountain Science Center, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA*
[3]*Montana Fish, Wildlife and Parks, 1400 South 19th, Bozeman, MT 59715, USA*
[4]*Resource Management Office, Grand Teton National Park, P.O. Box 170, Moose, WY 83012, USA*
[5]*Idaho Department of Fish and Game, 1515 Lincoln Road, Idaho Falls, ID 83401, USA*

Abstract: For many years, the primary strategy for managing grizzly bears (*Ursus arctos*) that came into conflict with humans in the Greater Yellowstone Ecosystem (GYE) was to capture and translocate the offending bears away from conflict sites. Translocation usually only temporarily alleviated the problems and most often did not result in long-term solutions. Wildlife managers needed to be able to predict the causes, types, locations, and trends of conflicts to more efficiently allocate resources for pro-active rather than reactive management actions. To address this need, we recorded all grizzly bear–human conflicts reported in the GYE during 1992–2000. We analyzed trends in conflicts over time (increasing or decreasing), geographic location on macro- (inside or outside of the designated Yellowstone Grizzly Bear Recovery Zone [YGBRZ]) and micro- (geographic location) scales, land ownership (public or private), and relationship to the seasonal availability of bear foods. We recorded 995 grizzly bear–human conflicts in the GYE. Fifty-three percent of the conflicts occurred outside and 47% inside the YGBRZ boundary. Fifty-nine percent of the conflicts occurred on public and 41% on private land. Incidents of bears damaging property and obtaining anthropogenic foods were inversely correlated to the abundance of naturally occurring bear foods. Livestock depredations occurred independent of the availability of bear foods. To further aid in prioritizing management strategies to reduce conflicts, we also analyzed conflicts in relation to subsequent human-caused grizzly bear mortality. There were 74 human-caused grizzly bear mortalities during the study, primarily from killing bears in defense of life and property (43%) and management removal of bears involved in bear–human conflicts (28%). Other sources of human-caused mortality included illegal kills, electrocution by downed power-lines, mistaken identification by American black bear (*Ursus americanus*) hunters, and vehicle strikes. This analysis will help provide wildlife managers the information necessary to develop strategies designed to prevent conflicts from occurring rather than reacting to conflicts after they occur.

Key words: beehives, conflict, defense of life and property, grizzly bear, human injury, livestock depredation, management, mortality, property damage, *Ursus arctos*, Yellowstone Ecosystem

Ursus 15(1):10–22 (2004)

For many years, records of grizzly bear–human conflicts in the GYE (Fig. 1) were dispersed among many agencies and individuals (Gunther et al. 2000*a*). These records varied in level of detail, criteria, and definition of terms used. This situation hindered consistent review of documented bear–human conflicts in the ecosystem and potentially delayed prediction, evaluation, correction, and prevention of grizzly bear–human conflict situations. In addition, the primary strategy for resolving conflicts was to capture and translocate the offending bears away from conflict sites. Translocation usually only temporarily alleviated the conflicts and most often did not result in long-term solutions (Knight et al. 1988, Meagher and Fowler 1989, Blanchard and Knight 1995). Translocated bears or

[6]kerry_gunther@nps.gov [7]mark_haroldson@usgs.gov
[8]kfrey@montana.edu [9]steve_cain@nps.gov
[10]Present address: U.S. Forest Service, Rocky Mountain Research Station, 800 E. Beckwith, Missoula, MT 59812, USA; jpcopeland@fs.fed.us [11]chuck_schwartz@usgs.gov

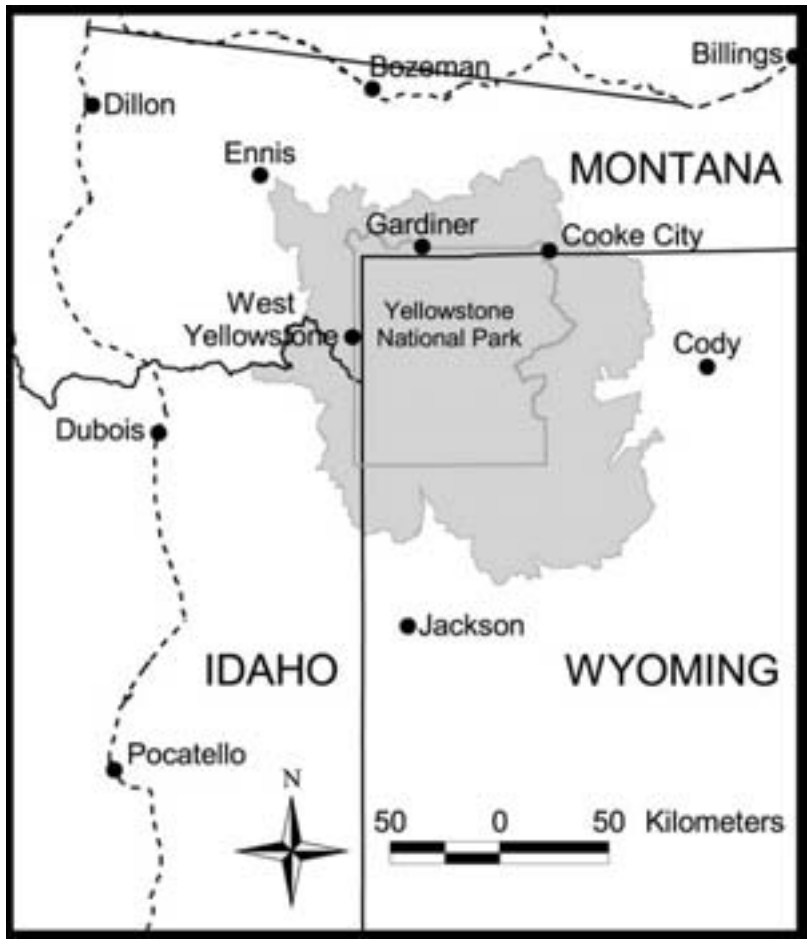

Fig. 1. Greater Yellowstone Ecosystem and Yellowstone Grizzly Bear Recovery Zone (shaded) in Idaho, Montana, and Wyoming, USA.

other bears frequently came into the same types of conflicts in the same areas repeatedly (Meagher and Fowler 1989). Repeated conflicts often resulted in grizzly bears being killed either by management agencies or private citizens. Prior to 1998, a high level of human-caused mortality (Haroldson and Frey 2002) was the primary factor preventing accomplishment of grizzly bear population recovery goals outlined in the Grizzly Bear Recovery Plan (U.S. Fish and Wildlife Service [USFWS] 1993).

Land and wildlife managers needed to be able to predict the causes, types, locations, and trends of conflicts to more efficiently allocate resources for management actions that prevent conflicts before they occur, rather than reacting to conflicts after they occur. In 1992, the Yellowstone Ecosystem Subcommittee (YES) of the Interagency Grizzly Bear Committee (IGBC) requested that agencies responsible for grizzly bear–human conflict management in the GYE compile reports annually that summarized conflicts and management actions (Gunther et al. 2000*a*). To address this request, we recorded all grizzly bear–human conflicts and management actions reported in the GYE during 1992–2000 and provided annual reports to the YES and IGBC.

Here we analyze all 9 years (1992–2000) of conflict data. Our objective was to reduce and prevent human-caused grizzly bear mortality and bear-caused human injuries, property damages, livestock depredations, and incidents of bears damaging gardens, orchards, and beehives through dissemination of information to the public and preventative rather than reactive management of grizzly bears. A second objective was to assist state and federal agencies as well as non-government organizations (NGOs) in setting priorities for allocating resources to reduce bear–human conflicts. Prioritization will enable available personnel and funding to focus on correcting the most prevalent types of bear–human conflicts in the GYE and those that most often result in bear mortality. In the past, high profile conflicts such as bear-inflicted human injuries often received much of the publicity and management response, even if these incidents were rare or did not lead to significant numbers of dead grizzly bears. Reduction of human-caused grizzly bear mortality and habitat protection are 2 of the most important conservation efforts that can lead to recovery and long-term viability of grizzly bears in the GYE.

Study area

Our study area encompassed the GYE, an area of over 34,416 km^2 occupied by grizzly bears in Wyoming, Montana, and Idaho, USA (Schwartz et al. 2002). The area includes land managed by Yellowstone (YNP) and Grand Teton national parks, and the Gallatin, Shoshone, Bridger-Teton, Targhee, Beaverhead, and Custer national forests, as well as state and private lands. Detailed descriptions of the study area can be found in Schwartz

et al. (2002), Haroldson et al. (2002), Craighead et al. (1995), and U.S. Fish and Wildlife Service (1993, 1994).

Methods

We recorded all grizzly bear–human conflicts reported in the GYE during 1992–2000. For analysis, we grouped similar types of conflicts into 5 broad categories: (1) property damage/anthropogenic foods, (2) gardens/orchards, (3) beehives, (4) livestock depredation, and (5) human injury. We defined "property damage/anthropogenic foods" as incidents where bears damaged personal property including camping equipment, vehicles, homes, cabins, barns, sheds, pets, or other personal property or incidents where bears obtained human foods, beverages, garbage, grease, pet food, bird seed, livestock feed, or other edible human-related attractants. "Gardens/orchards" were incidents where grizzly bears damaged or obtained fruits or vegetables from gardens or orchards. We defined "beehives" as incidents where grizzly bears damaged or obtained honey from domestic beehives, colonies, or apiaries. "Livestock depredation" was defined as incidents where grizzly bears killed or injured domestic cattle, sheep, horses, mules, burros, donkeys, ducks, geese, turkeys, chickens, or other domestic livestock, excluding pets. "Human injury" was defined as incidents where grizzly bears killed or injured people, including minor scratches and bites.

We also recorded all known human-caused grizzly bear mortalities that occurred during the study. We defined "known mortality" as those determined by radio telemetry or carcass recovery (Knight et al. 1988). The term "defense of life or property (DLP)" was defined as incidents where private citizens killed bears in defense of life or personal property. "Management removal" was defined as the planned lethal or non-lethal removal of bears from the wild by agency personnel due to conflicts with people. "Illegal kill" was defined as incidents of malicious killing, radiocollars found cut off of marked bears, and bears killed and left in the field unreported. "Mistaken identification by black bear hunter" included all incidents where grizzly bears were identified as American black bears and taken by licensed hunters during the black bear hunting season. We defined "vehicle strike" as incidents where grizzly bears were hit and killed by vehicles. "Accidental management death" was defined as incidents where bears were killed unintentionally during management-related capture, trapping, handling, aversive conditioning, or hazing.

In the GYE, availability of the more concentrated and preferred grizzly bear plant and animal foods normally fluctuate unpredictably from year to year (Craighead et al. 1995). Due to these perturbations, no major seasonal foods are highly abundant every year. The major high quality, concentrated food sources in the GYE include winter-killed ungulate carcasses (Green et al. 1997), newborn elk calves (*Cervus elaphus*, [Gunther and Renkin 1990]), spawning cutthroat trout (*Oncorhynchus clarki*, [Reinhart and Mattson 1990]), army cutworm moths (*Euxoa auxiliaris*, [Mattson et al. 1991*a*, Bjornlie and Haroldson 2002]), and whitebark pine seeds (*Pinus albicaulis* [Mattson et al. 1992]). In addition, although of lower caloric value and less concentrated than ungulates, trout, army cutworm moths, and whitebark pine seeds, roots of yampa (*Perideridia gairdneri*), biscuit root (*Lomatium cous*), and sweet cecily (*Osmorhiza chilensis*) are eaten extensively by GYE grizzly bears during some years and seasons (Mattson et al. 1991*b*). We qualitatively classified the abundance of these and other seasonal bear foods as good, average, or poor. Our qualitative estimates were derived by experienced biologists through diagnostic field sign (feed sites, scats) observed during thousands of hours conducting grizzly bear research and monitoring activities and managing bear–human conflicts throughout the GYE. Craighead et al. (1995) used similar qualitative estimates to measure food abundance.

We classified bear seasons based on major changes in bear behavior and food habits as defined for the GYE by Mattson et al. (1999). Spring was defined as the period from den emergence through 15 May. Winter-killed ungulate carcasses are the primary, high quality bear food during spring (Green et al. 1997). Estrus was considered 16 May–15 July. Activities associated with reproduction (travel, leisure, and play) dominate most behavior during this period (Mattson et al. 1991*b*). The primary high quality bear foods consumed during estrus are over-wintered whitebark pine seeds when present, elk calves (Gunther and Renkin 1990), and spawning cutthroat trout (Reinhart and Mattson 1990). We defined early hyperphagia as the period 16 July–31 August. This season is characterized by the onset of hyperphagia (Nelson et al. 1983) and consumption of army cutworm moths (Mattson et al. 1991*a*), over-wintered whitebark pine nuts when present (Mattson et al. 1992), and roots (Mattson et al. 1991*b*). The late hyperphagia season was defined as from 1 September through den entrance. The primary high quality bear foods during this season are army cutworm moths (Mattson et al. 1991*a*) and the current year's whitebark pine seeds (Mattson et al. 1992). When the availability of whitebark pine seeds is below average during late hyperphagia, ungulate meat (Mattson

Table 1. Grizzly bear–human conflicts reported by season in the Greater Yellowstone Ecosystem, 1992–2000.

Season	Human injury	Property damage/ anthropogenic foods	Gardens and orchards	Beehives	Livestock depredations	Total
Spring	1	32	0	5	6	44
Estrus	4	73	1	6	70	154
Early hyperphagia	7	133	3	10	251	404
Late hyperphagia	23	209	40	12	109	393
Total	35	447	44	33	436	995

1997) and roots (our observations) become more prominent in the diet of GYE grizzly bears.

For each type of conflict, we used linear regression calculated with SYSTAT software (Wilkinson 1988) to analyze annual trends in the number of incidents (increasing or decreasing), location on a macro (inside or outside of the YGBRZ) scale, and land ownership (public or private). We considered $P < 0.05$ to be significant. To identify areas with concentrations of conflicts and human-caused grizzly bear mortalities, we calculated the 80% conflict and mortality distribution isopleths using the fixed kernel estimator with the software package Animal Movements (Hooge and Eichenlaub 1997). To analyze the relationship between the number of conflicts and the annual and seasonal availability of non-anthropogenic bear foods, we used *K*-means cluster analysis (Kachigan 1982), calculated with SYSTAT software (Wilkinson 1988), to group qualitative measures (good, average, poor) of seasonal (spring, estrus, early hyperphagia, late hyperphagia) grizzly bear food availability with the number of incidents of property damage/anthropogenic foods and livestock depredations. The variables that contributed significantly to the grouping were identified where $P < 0.05$. There were too few incidents of gardens/orchards, beehives, and human injury to meaningfully group by season, food availability, and number of conflicts.

Results

Grizzly bear–human conflicts

During 1992–2000, 995 grizzly bear–human conflicts were reported in the GYE. These conflicts included incidents of property damage/anthropogenic foods (45%, $n = 447$), livestock depredation (44%, $n = 436$), gardens/orchards (4%, $n = 44$), human injury (4%, $n = 35$), and beehives (3%, $n = 33$). Fifty-nine percent ($n = 589$) of the conflicts occurred on public land and 41% ($n = 406$) on private land. Fifty-three percent ($n = 527$) of the conflicts occurred outside and 47% ($n = 468$) inside of the YGBRZ.

Bear–human conflicts by season. The number of conflicts generally increased from spring through early and late hyperphagia (Table 1). Livestock depredations peaked during early hyperphagia. The number of conflicts involving property damage/anthropogenic foods, human injuries, gardens/orchards, and beehives all had similar patterns, peaking during late hyperphagia.

Bear–human conflicts by month. Relatively few of the 995 grizzly bear–human conflicts occurred in March ($n = 3$) and April ($n = 24$), months when bears were emerging from dens (Haroldson et al. 2002), or in November ($n = 10$), just prior to den entrance (Table 2). Ninety-six percent ($n = 958$) of the conflicts occurred from May through October, the primary months when GYE grizzly bears are active (Haroldson et al. 2002). The number of conflicts increased from March through August and September, then decreased from October through November. No conflicts were reported during December, January, or February, when most bears in the GYE are in winter dens (Haroldson et al. 2002). The peak in livestock depredations occurred in August, whereas the peak in incidents of property damage/anthropogenic foods, human injuries, and gardens/orchards occurred in September. Damage to beehives had a less well defined peak; however, most occurred from July–October.

Relationship between conflicts and bear foods. Cluster analysis of seasonal bear food availability and incidents of property damage/anthropogenic foods identified 2 sub-groups with minimal within sub-group variation but maximal between sub-group variation. Seasons when bear food availability was either average or good grouped with low numbers of property damage/anthropogenic foods. In contrast, seasons when the availability of bear foods was poor grouped with high numbers of property damage/anthropogenic foods (Table 3). There was a significant association (Fig. 2) between the number of incidents of property damage/anthropogenic foods and grizzly bear food availability during spring ($F = 7.00$, 7 df, $P = 0.033$), early hyperphagia ($F = 6.481$, 7 df, $P = 0.038$), and late hyperphagia ($F = 29.167$,

Table 2. Grizzly bear–human conflicts reported by month in the Greater Yellowstone Ecosystem, 1992–2000.

Month	Human injury	Property damage/ anthropogenic foods	Gardens and orchards	Beehives	Livestock depredations	Total
January	0	0	0	0	0	0
February	0	0	0	0	0	0
March	0	3	0	0	0	3
April	1	18	0	4	1	24
May	1	36	0	2	10	49
June	2	23	1	3	15	44
July	4	51	0	6	133	194
August	4	107	3	6	168	288
September	17	147	23	5	84	276
October	5	57	17	6	22	107
November	1	5	0	1	3	10
December	0	0	0	0	0	0
Total	35	447	44	33	436	995

7 df, $P = 0.001$). Food availability during estrus ($F = 0.333$, 7 df, $P = 0.582$) did not contribute significantly to the number of incidents of property damage/anthropogenic foods. When the availability of natural bear foods was rated as average or good, there was an average of 27 (range 13–33) incidents of property damage/anthropogenic foods annually. Conversely, when the availability of natural bear foods was rated as poor, there was an average of 94 (range 73–124) incidents of property damage/anthropogenic foods annually. Livestock depredations (Fig. 3) were not associated with the seasonal availability of natural bear foods during spring ($F = 1.340$, 7 df, $P = 0.285$), estrus ($F = 0.605$, 7 df, $P = 0.462$), early hyperphagia ($F = 1.089$, 7 df, $P = 0.331$), or late hyperphagia ($F = 0.032$, 7 df, $P = 0.862$) (Table 3).

Location of conflicts. The conflict distribution map constructed using the fixed kernel 80% isopleth identified 6 polygons where concentrations of conflicts occurred (Fig. 4). These 6 polygons contained 756 of the 995 (76%) conflicts. Areas with concentrations of conflicts included: (1) the Headwaters of the Snake, Green, and Wind river drainages ($n = 323$), where bears killed cattle and sheep, damaged property, and obtained anthropogenic foods; (2) the North and South Forks of the Shoshone River ($n = 260$), where bears damaged property and beehives, obtained anthropogenic foods, and killed cattle and sheep; (3) the Yellowstone River area ($n = 66$), where bears damaged gardens and orchards and obtained anthropogenic foods; (4) the Badger Creek and Leigh Creek area ($n = 48$), where bears killed sheep; (5) the Hebgen Lake and South Fork Madison River area ($n = 33$), where bears damaged property and obtained anthropogenic foods; and (6) the Taylors Fork area ($n = 26$), where bears damaged property and obtained anthropogenic foods.

Property damage/anthropogenic foods. Incidents of grizzly bears damaging property, obtaining anthropogenic foods, or both comprised 45% ($n = 447$) of all conflicts reported. Incidents of property damage/anthropogenic foods occurred both inside ($n = 274$) and outside ($n = 173$) the YGBRZ and on public ($n = 196$) and private ($n = 251$) land. Incidents where grizzly bears damaged property but did not obtain food included damage to equipment ($n = 41$), buildings ($n = 37$), vehicles ($n = 25$), and other personal property ($n = 11$). Incidents where grizzly bears obtained anthropogenic foods included raiding of garbage ($n = 122$), livestock and pet foods ($n = 110$), human foods ($n = 94$), and other anthropogenic attractants ($n = 7$). Most (77%) incidents of property damage/anthropogenic foods occurred during early (30%, $n = 133$) and late (47%, $n = 209$) hyperphagia (Table 1). The number of incidents of property damage/anthropogenic foods varied greatly between years and did not increase or decrease significantly over the duration of the study ($\beta = 1.08$, $F = 0.05$, $P = 0.83$), inside ($\beta = 1.63$, $F = 0.45$, $P = 0.52$), or outside ($\beta = -0.55$, $F = 0.03$, $P = 0.86$) of the YGBRZ, or on public ($\beta = 0.08$, $F = 0.002$, $P = 0.96$) versus private ($\beta = 1.00$, $F = 0.08$, $P = 0.78$) land.

Livestock depredations. Incidents of depredation on livestock comprised 44% ($n = 436$) of the total conflicts reported. Livestock depredations included incidents with cattle (71%, $n = 311$), sheep (27%, $n = 116$), horses ($n = 3$), chickens ($n = 3$), ducks ($n = 2$), and turkeys ($n = 1$). Livestock depredations occurred on public (80%, $n = 349$) and private (20%, $n = 87$) land, both inside (31%, $n = 134$) and outside (69%, $n = 302$) the YGBRZ. All incidents of grizzly bears depredating horses, chickens, ducks, and turkeys occurred on private land. Multiple kills within a single incident were common when grizzly bears

Table 3. Qualitative assessment of seasonal bear foods and number of grizzly bear–human conflicts reported in the GYE, 1992–2000.

Year	Spring	Estrus	Early hyperphagia	Late hyperphagia	Property damage/ anthropogenic foods	Gardens/ orchards	Beehives	Human injury	Livestock depredations
1992	Average	Average	Average	Good[a]	13	0	0	3	8
1993	Average	Average	Average[b]	Average[bc]	33	7	0	0	50
1994	Poor[d]	Poor[e]	Poor[fg]	Poor[gh]	124	5	5	9	22
1995	Average	Poor[e]	Poor[f]	Poor[h]	73	9	14	3	42
1996	Average	Poor[e]	Average	Good[a]	22	0	1	2	49
1997	Good[i]	Good[j]	Good[j]	Average[k]	31	7	0	8	73
1998	Average	Average	Average	Good[a]	33	6	3	4	71
1999	Good[i]	Average	Average	Good[a]	32	3	4	2	72
2000	Poor[d]	Good[j]	Average[l]	Poor[gh]	86	7	6	4	49

[a]Current year's whitebark pine seed crop.
[b]Low numbers of army cutworm moths at high elevation moth aggregation sites but above average precipitation, which resulted in good forb and graminoid foliage and good root crops that were eaten by bears during early and late hyperphagia.
[c]Average whitebark pine seed crop, current year.
[d]Low number of winter-killed ungulate carcasses.
[e]Low number of spawning cutthroat trout.
[f]Low number of army cutworm moths at high elevation moth aggregation sites.
[g]Hot, dry summer caused vegetation to desiccate early.
[h]Poor whitebark pine seed crop, current year.
[i]High number of winter-killed ungulate carcasses.
[j]Over-wintered whitebark pine seeds left over from the previous fall.
[k]Poor whitebark pine seed crop, but above average precipitation resulted in good forb and graminoid foliage and good root crops that were eaten by bears during early and late hyperphagia.
[l]Over-wintered whitebark pine seeds left over from the previous fall early in season, but hot, dry summer caused most vegetal bear foods to desiccate early.

depredated sheep (59%, 68 of 116 incidents), chickens (3 of 3 incidents), ducks (2 of 2 incidents), and turkeys (1 of 1 incident), but rare when they preyed on cattle (2%, 7 of 311 incidents) and horses (0 of 3 incidents). With sheep, 1 to 133 sheep were killed and averaged 4.3 sheep/incident. With cattle, 1 to 3 cows were killed and averaged 1.03 deaths/incident. Most livestock depredations occurred during early (58%, $n = 251$) and late (25%, $n = 109$) hyperphagia (Table 1). The number of incidents of

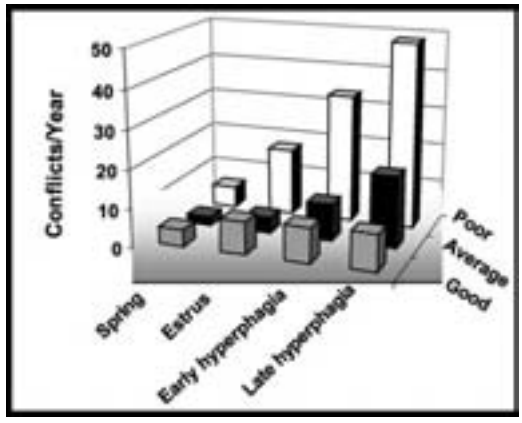

Fig. 2. Relationship between qualitative assessment of high quality seasonal bear foods and the number of incidents of property damage/anthropogenic foods in the Greater Yellowstone Ecosystem, 1992–2000.

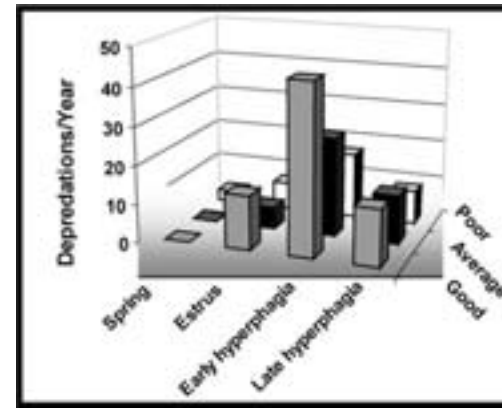

Fig. 3. Relationship between qualitative assessment of high quality seasonal bear foods and the number of livestock depredations in the Greater Yellowstone Ecosystem, 1992–2000.

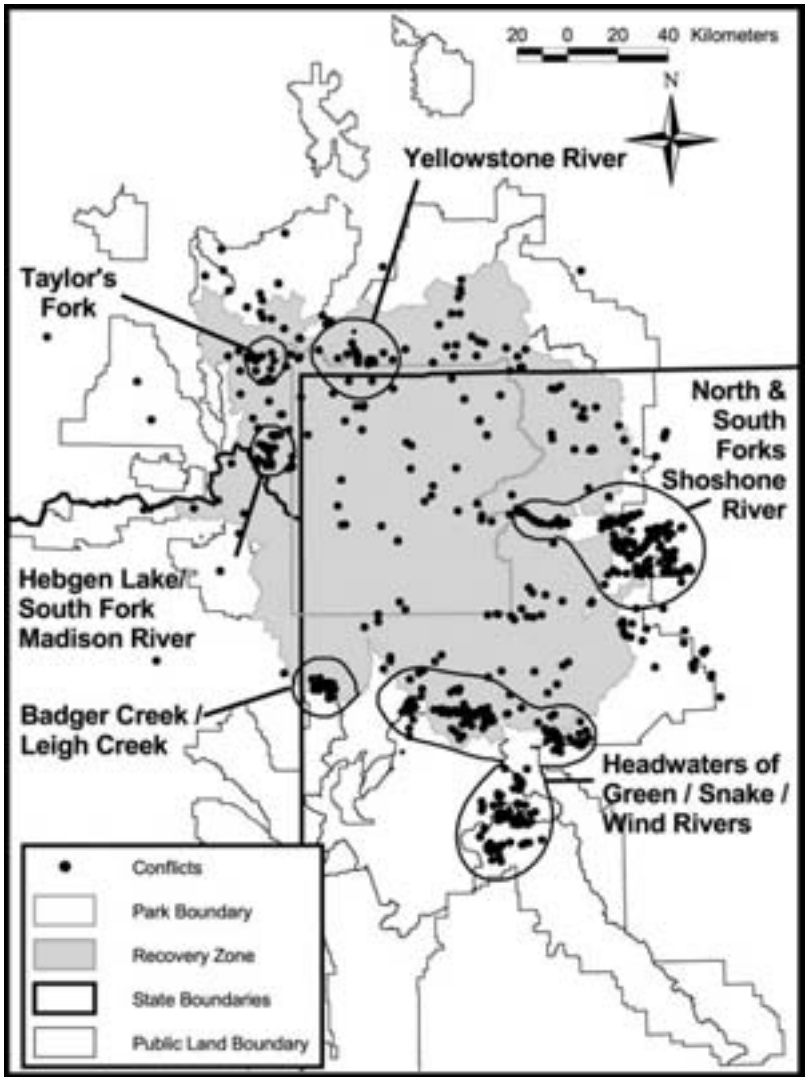

Fig. 4. Fixed kernel distribution constructed with locations of grizzly bear–human conflicts in the Greater Yellowstone Ecosystem, 1992–

livestock depredation increased (Fig. 5) significantly from 1992 through 2000 ($\beta = 5.98$, $F = 7.92$, $P = 0.02$). Livestock depredations increased significantly outside of the YGBRZ ($\beta = 7.12$, $F = 29.08$, $P = 0.01$) and on private land ($\beta = 2.00$, $F = 11.05$, $P = 0.01$), but not inside the YGBRZ ($\beta = -1.13$, $F = 0.94$, $P = 0.36$). There was also a strong increasing trend for livestock depredations on public land ($\beta = 3.98$, $F = 3.65$, $P = 0.09$).

Gardens/orchards. Forty-four incidents were reported in which grizzly bears damaged gardens ($n = 6$) or orchards ($n = 38$). Twenty-nine of the incidents occurred inside and 15 outside of the YGBRZ. Thirty-two of the incidents occurred on private and 12 on public lands. Most (91%, $n = 40$) damage to gardens/orchards occurred during late hyperphagia (Table 1). The number of incidents of gardens/orchards was highly variable between years and did not increase or decrease significantly over the study ($\beta = 0.27$, $F = 0.38$, $P = 0.55$), inside ($\beta = 0.08$, $F = 0.05$, $\beta = 0.08$, $P = 0.83$) or outside ($\beta = 0.18$, $F = 0.44$, $P = 0.52$) of the YGBRZ, or on public ($\beta = 0.03$, $F = 0.03$, $P = 0.87$) versus private ($\beta = 0.23$, $F = 0.32$, $P = 0.58$) land.

Human injury. Grizzly bears injured 38 people in 35 incidents (3 incidents involved 2 people; the remainder involved single individuals). No people were killed by grizzly bears during the study. Thirty-one (89%) injuries occurred inside and 4 outside of the YGBRZ. Thirty-two (91%) of the incidents of grizzly bear-inflicted human injury occurred on public and 3 on private land. Grizzly bear-inflicted human injuries involved hunters (54%, $n = 19$), hikers (31%, $n = 11$), people in campsites ($n = 2$), a jogger ($n = 1$), a man on foot leading a mule ($n = 1$), and a man sitting on the ground eating lunch near his horse ($n = 1$). Most (66%, $n = 23$) grizzly bear-inflicted human injuries occurred during late hyperphagia (Table 1). The number of incidents of human injury was highly variable between years and did not increase or decrease significantly over the duration of the study ($\beta = 0.08$, $F = 0.044$, $P = 0.84$), inside ($\beta = -0.03$, $F = 0.01$, $P = 0.92$) or outside ($\beta = 0.12$, $F = 0.77$, $P = 0.40$) of the YGBRZ, or on public ($\beta = 0.05$, $F = 0.02$, $P = 0.89$) versus private ($\beta = 0.03$, $F = 0.12$, $P = 0.74$) land.

Beehives. Thirty-three incidents of damage to beehives were reported; all occurred on private land outside of the YGBRZ. Most damage to beehives occurred during early ($n = 10$) and late ($n = 12$) hyperphagia (Table 1). The number of incidents on beehives was highly variable between years and did not increase or decrease significantly over the duration of the study ($\beta = 0.30$, $F = 0.24$, $P = 0.63$), outside ($\beta = 0.30$, $F = 0.24$, $P = 0.64$) of the YGBRZ, or on private land ($\beta = 0.30$, $F = 0.24$, $P = 0.64$).

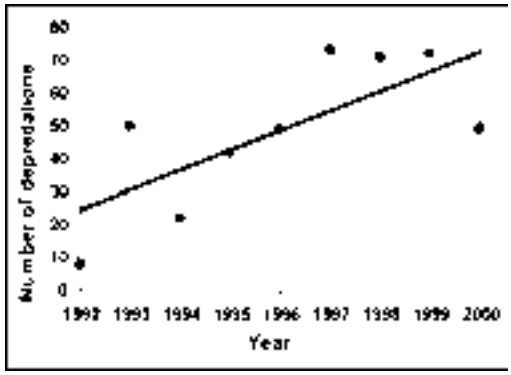

Fig. 5. Incidents of livestock depredation in the Greater Yellowstone Ecosystem by year, 1992–2000.

There were no conflicts involving beehives inside of the YGBRZ or on public land during the study.

Human-caused grizzly bear mortality

There were 74 known incidents of human-caused grizzly bear mortality in the GYE during 1992–2000 (Table 4). Killing of bears in defense of life and property (43%, $n = 32$) and management removal (28%, $n = 21$) of bears involved in bear–human conflicts were the most prevalent sources of human-caused mortality. Other sources included illegal kills ($n = 9$), mistaken identification by black bear hunters ($n = 5$), electrocution by downed power-lines ($n = 3$), collisions with vehicles ($n = 2$), and accidental deaths during management actions ($n = 2$). Most (61%) human-caused grizzly bear mortality occurred during late hyperphagia (Table 4). Human-caused grizzly bear mortality was scattered throughout the GYE (Fig. 6). No distinct geographic concentrations of human-caused grizzly bear mortalities were identified using the fixed kernel 80% mortality distribution isopleth.

Grizzly bears were more likely to die (Table 5) when involved in bear-inflicted human injuries (one dead bear/4 incidents), than when obtaining anthropogenic foods (1 dead bear/24 incidents), damaging property (1 dead bear/38 incidents), depredation on sheep (1 dead bear/39 incidents), or depredation on cattle (1 dead bear/104 incidents). During the study period, no grizzly bears died directly due to depredation on chickens, ducks, and turkeys, or damage to gardens, orchards, or beehives.

Grizzly bears killed in defense of human life or property ($n = 32$) were the highest source of human-caused grizzly bear mortality recorded during the study. Defense of life kills included incidents with hunters ($n = 28$) and an incident at a cabin ($n = 1$). Defense of property kills ($n = 3$) included incidents of protecting horses ($n = 1$) and dogs ($n = 1$) at private residences and sheep ($n = 1$) on public land grazing allotments. Most incidents where grizzly bears were killed in self defense occurred inside the YGBRZ (97%, $n = 28$) and on public land (93%, $n = 26$). All defense of property incidents occurred outside of the YGBRZ. Most (84%, $n = 27$) DLP kills occurred during late hyperphagia, especially in September and October (Table 6), coinciding with big game hunting seasons in the GYE.

Removals by state and federal management agencies of bears involved in conflicts ($n = 21$) was the second highest source of human-caused grizzly bear mortality. These included removal of grizzly bears involved in property damage/anthropogenic foods ($n = 15$), livestock depredations ($n = 5$, 3 cattle, 2 sheep), and human injuries ($n = 1$). Most management removals occurred outside of the YGBRZ (57%, $n = 12$) and on private land (62%, $n = 13$) and occurred during early (48%, $n = 10$) and late (38%, $n = 8$) hyperphagia from August through October (Table 6).

Nine grizzly bears were killed illegally. All illegal kills occurred inside the YGBRZ; 8 of 9 incidents occurred on public land and 1 on private land. Most illegal kills ($n = 6$) occurred during late hyperphagia. Five grizzly bears were mistaken for black bears and killed by licensed hunters during the black bear hunting season. Three occurred on public and 2 on private land; 2 occurred inside and 3 outside of the YGBRZ. Grizzly bears were also killed by downed powerlines ($n = 3$) and vehicle collisions ($n = 2$); all occurred on public land inside the YGBRZ.

Table 4. Human-caused grizzly bear mortality in the Greater Yellowstone Ecosystem by season, 1992–2000.

Season	Defense of life or property	Management removal	Illegal	Black bear hunter	Powerline	Vehicle strike	Accidental	Total
Spring	2	0	2	2	0	0	0	6
Estrus	1	3	1	0	0	1	0	6
Early hyperphagia	2	10	0	1	3	0	1	17
Late hyperphagia	27	8	6	2	0	1	1	45
Total	32	21	9	5	3	2	2	74

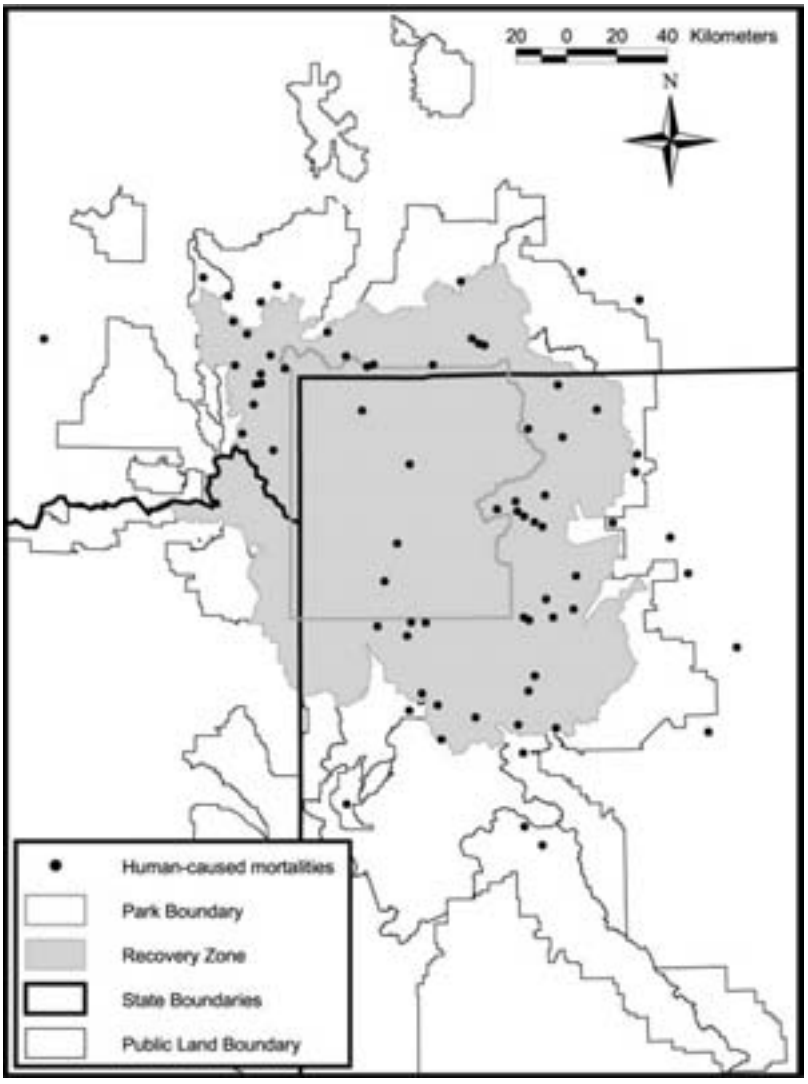

Fig. 6. Distribution of human-caused grizzly bear mortalities in the Greater Yellowstone Ecosystem, 1992–2000. The shaded area represents the Yellowstone Grizzly Bear Recovery Zone.

Two grizzly bears died during management handling accidents. Both were related to incidents that occurred outside the YGBRZ on private land.

Discussion

Incidents of bears damaging property or obtaining anthropogenic foods were the most prevalent types of conflicts recorded during the study. Approximately 1 of 38 incidents of property damage and 1 of 24 incidents of bears obtaining human foods, garbage, or livestock and pet foods resulted in dead bears. Grizzly bears were more likely to die when they obtained anthropogenic foods because a food reward often led to repeated visits and conflicts at the same site. Once a bear successfully obtains a food reward at a particular location, the site is usually periodically re-checked for more food (Stokes 1970, Meagher and Phillips 1983).

Incidents of property damage/anthropogenic foods generally increased from early spring throughout the active bear season and peaked during late hyperphagia. The numbers of these types of conflicts varied annually and were inversely related to the annual and seasonal abundance of high quality bear foods. This association was strongest during late hyperphagia. When the availability of concentrated, high quality bear foods was poor, the number of incidents of bears damaging property and obtaining anthropogenic foods was generally high. In contrast, when the availability of bear foods was rated as average or good, the number of these types of conflicts was generally low. Thus, it is likely that the energetic needs associated with hyperphagia, as bears attempted to put on weight prior to hibernation (Nelson et al. 1983), sometimes lead bears to seek foods associated with human activities. Nutritional stress associated with failure of natural bear foods, especially during late-hyperphagia, significantly magnifies this problem. The inverse association between bear foods and bear–human conflicts is consistent with the inverse correlation between whitebark pine seed production and human-caused grizzly bear mortality documented in the GYE by Mattson et al. (1992).

The range occupied by grizzly bears has expanded by 48% since 1970, and grizzly bears now occupy areas outside the YGBRZ (Schwartz et al. 2002). During 1992–2000, over half (53%) of all grizzly bear–human conflicts reported in the GYE occurred outside the designated YGBRZ. As grizzly bear range has expanded beyond the YGBRZ boundary (Schwartz et al. 2002), more spatial overlap with private land has occurred.

Table 5. Number of grizzly bear–human conflicts, human-caused grizzly bear mortalities associated with conflicts, and ratio of mortalities to conflicts in the Greater Yellowstone Ecosystem, 1992–2000.

Type of conflict	Bear mortality related to conflicts	Number of conflicts	Bear mortality: conflicts
Human injury	9	35	1:4
Anthropogenic foods	14	333	1:24
Property damage	3	113	1:38
Sheep depredation	3	116	1:39
Cattle depredation	3	311	1:104
Gardens/orchards	0	44	
Beehives	0	33	

During 1992–2000, almost half (41%) of all grizzly bear–human conflicts occurred on private land. If the range occupied by grizzly bears outside of the YGBRZ continues to expand, conflicts on both public and private land outside of the YGBRZ will likely increase as well.

Livestock depredation was the second most common type of conflict reported and was also the one type of conflict that increased significantly during 1992–2000. Livestock-killing grizzly bears appeared to kill cattle and sheep regardless of the abundance of natural bear foods. Most of the increase in livestock depredations occurred outside of the YGBRZ, both on public and private land. At present, highly selective control of livestock-killing grizzly bears has resulted in management removal of only the most chronic livestock killers. Approximately one grizzly bear dies for every 39 sheep and 104 cattle depredation incidents. The higher mortality rate for sheep-killing bears is likely due to the higher incidence of multiple kills on sheep (4.3 animals/incident) than cattle (1.03 animals/incident). Permanent removal of chronic depredators has been the most effective method of alleviating livestock losses while having minimal impact on the long-term survival of the grizzly bear population (Anderson et al. 2002). We predict that livestock depredations will likely continue to increase if the area occupied by grizzly bears outside of the YGBRZ continues to increase. The interface areas between occupied grizzly bear habitat and agricultural areas with livestock are likely to be a continual challenge to grizzly bear managers in the GYE.

Incidents of damage to gardens, orchards, and beehives comprised only a small proportion (<10%) of the total conflicts and resulted in no direct bear mortalities. Almost all incidents where grizzly bears damaged gardens and orchards occurred in late hyperphagia, coinciding with the season when garden and orchard fruits and vegetables are ripe and provide the greatest nutrition. Grizzly bears damaged beehives during all seasons, although there was a slight increase during early and late hyperphagia. Damage to gardens, orchards, and beehives is relatively easy to prevent with electric fencing. The state of Wyoming has successfully used electric fences to reduce incidents of grizzly bear damage to beehives. The state of Montana has expanded this technique to reduce conflicts at gardens, orchards, and garbage facilities on private land. Funding and personnel shortages have been the primary limiting factors in constructing electric fencing at conflict sites. Dedicating more resources to bear-proofing gardens, orchards, and beehives could further reduce these types of conflicts throughout the GYE.

Grizzly bear-inflicted human injuries also comprised only a small proportion (3%) of total conflicts. However, bear-inflicted human injuries received substantial pub-

Table 6. Human-caused grizzly bear mortality in the Greater Yellowstone Ecosystem by month, 1992–2000.

Month	Defense of life or property	Management removal	Illegal	Black bear hunter	Powerline	Vehicle strike	Accidental	Total
January	0	0	0	0	0	0	0	0
February	0	0	0	0	0	0	0	0
March	0	0	0	0	0	0	0	0
April	0	0	0	0	0	0	0	0
May	2	0	2	2	0	0	0	6
June	0	0	1	0	0	1	0	2
July	1	4	0	0	0	0	0	5
August	1	9	0	1	3	0	1	15
September	14	3	2	1	0	1	1	22
October	13	4	2	1	0	0	0	20
November	1	1	0	0	0	0	0	2
December	0	0	0	0	0	0	0	0
Unknown[a]	0	0	2	0	0	0	0	2
Total	32	21	9	5	3	2	2	74

[a]In 2 incidents, month of death could not be determined for the grizzly bear carcass.

licity during the study and likely contributed to excessive fear of grizzly bears by the public. Fear of being mauled by a grizzly bear likely contributed to some self-defense kills of grizzly bears. Approximately 1 grizzly bear died/4 people injured by bears. Most (8 of 9) grizzly bears that were killed after injuring people were killed by private citizens during the confrontation. These bear mortalities would be hard to prevent. However, many more grizzly bears died during encounters with people in which no one was hurt ($n = 24$). These types of incidents can probably be reduced, but not eliminated, in areas where grizzly bear habitat and recreational activity overlap.

Five grizzly bears were mistaken for black bears and killed by hunters during the black bear hunting season. These incidents likely had little influence on population trend but may have contributed to erosion of public support for hunting and can likely be reduced with improved hunter education.

Grizzly bears were also killed by downed powerlines ($n = 3$) and vehicle strikes ($n = 2$). These were rare occurrences and likely had little influence on population trend. However, the frequency of vehicle strike mortalities will likely increase as roads are widened and straightened to accommodate human safety concerns and the increase in human occupancy and recreational visitation to the GYE. Vehicle speed has been linked to the frequency of vehicle strike mortality of large mammals (Gunther et al. 2000*b*).

Management recommendations

Grizzly bears in the GYE have expanded their range considerably since being listed as threatened in 1975, and they now occupy areas beyond the designated YGBRZ boundary (Schwartz et al. 2002). Efforts to prevent bears from obtaining human foods and garbage have not kept pace with grizzly bear range expansion. To reduce bear–human conflict on public lands outside the YGBRZ, food and garbage storage orders should be expanded to areas where state management plans have identified grizzly bear occupancy as biologically feasible and socially acceptable.

Range expansion (Schwartz et al. 2002) has also resulted in spatial overlap of grizzly bears with privately owned land. To protect the core grizzly bear population, reduction of conflicts on private land within and immediately adjacent to the YGBRZ should be a high priority for wildlife management agencies and NGOs. In areas far beyond the YGBRZ boundary where state management plans indicate that grizzly bear occupancy is not biologically feasible or socially acceptable, nuisance bears should be controlled in a timely and effective manner.

The majority (76%) of grizzly bear–human conflicts occurred in 6 locations of human activity (see *Location of conflicts* section). Most of these 6 areas were recognized as population sinks by Knight et al. (1988) more than a decade ago. These 6 areas should be a high priority for wildlife management agencies and NGOs when allocating resources for reducing grizzly bear–human conflicts in the GYE.

Most (71%) livestock depredations involve cattle, and almost all cattle depredations occur in the state of Wyoming. Very few cattle depredations occur in Montana despite presence and range overlap between grizzly bears and cattle. We recommend further analysis of livestock depredation data and cattle husbandry practices between the areas to determine if current practices in Wyoming could be modified to reduce cattle depredation by grizzly bears in a cost-effective manner for livestock producers.

Grizzly bears and domestic sheep are generally not compatible (Knight and Judd 1983). Sheep depredation accounted for over one-fourth (27%) of all incidents of livestock depredation in the GYE during 1992–2000. NGOs in partnership with federal agencies have successfully used financial incentives, offered to willing participants, to get permittees to retire sheep grazing allotments on public land. We recommend further use of these types of partnerships with NGOs to retire sheep grazing allotments held by willing participants on public land inside the YGBRZ. Outside of the YGBRZ and on private land, we recommend use of electric fence to protect domestic sheep at night on bed-grounds at both remote backcountry allotments and rural ranches. Electric fencing has potential to protect sheep from grizzly bears at night on bed-grounds where most depredations occur (Debolt 2000).

Electric fencing also has been used successfully to reduce conflicts at gardens, orchards, beehives, and garbage storage facilities on private land. Partnerships with NGOs to provide electric fencing and assist rural landowners with fence installation and maintenance on private land should be explored.

Although bear-inflicted human injuries comprise only a small proportion of total conflicts, they generate a disproportionate amount of negative press about grizzly bears, and DLP kills by hunters comprise a significant proportion of total human-caused grizzly bear mortality. Wildlife management agencies need to improve methods to inform hunters and recreationists in grizzly bear habitat about bear behavior and methods to reduce encounters

and defuse confrontations when they occur. They should also promote the use of bear repellent spray as a nonlethal alternative for stopping aggressive encounters. Bear repellent sprays containing capsicum are useful in repelling aggressive bears in many situations (Herrero and Higgins 1998).

Although relatively few grizzly bears were mistaken for black bears and killed by black bear hunters, these incidents erode public support for hunting and can likely be reduced. Methods to teach bear species identification as well as the current distribution of grizzly bears in the GYE should be improved to reduce the frequency of these mortalities. Hunter education should also include areas where grizzly bear range is likely to expand in the near future, rather than just currently occupied habitat.

Grizzly bear–human conflicts often lead to human-caused bear mortality. During our study, human-caused bear mortality was low enough to allow the GYE grizzly bear population to increase (Haroldson and Frey 2002), expand its range (Schwartz et al. 2002), and meet all demographic population goals (Haroldson and Frey 2002) outlined in the Grizzly Bear Recovery Plan (USFWS 1993). Although all population goals are currently being achieved, reduction of grizzly bear–human conflicts is still warranted. In addition to contributing to bear mortality, grizzly bear–human conflicts erode public support for grizzly bear conservation. By reducing grizzly bear–human conflicts and bear-inflicted human injuries, public support for bears can be enhanced and human-caused bear mortalities reduced. Greater public acceptance of grizzly bears may also increase support for protection of habitat and further expansion of grizzly bear range in the GYE. The larger the area grizzly bears are allowed to occupy in the GYE, the less vulnerable the population will be to long-term climate, habitat, pathogen, or human-induced changes in carrying capacity (Mattson and Reid 1991). Several important grizzly bear foods in the GYE, including whitebark pine seeds and cutthroat trout, are currently threatened due to human activities and the introduction of exotic organisms (Mattson and Reid 1991, Gunther et al. 1995, Mattson 2000, Reinhart et al. 2001).

Acknowledgments

Several people contributed toward completion of this paper. M. Bruscino provided conflict data from the Wyoming portion of the GYE. R. Renkin conducted linear regression and *K*-means cluster analysis of the data. We thank reviewers J. Claar and R. Mattson as well as Editor R. Harris, Associate Editor R. Shideler, and Technical Editor M. Munson-McGee for comments that improved this manuscript. R. Gray provided helpful editorial comments. S. Chin produced the figures. We also thank all the dedicated people who assisted with management of grizzly bear–human conflicts in the GYE.

Literature cited

ANDERSON, C.R., M.A. TERNENT, AND D.S. MOODY. 2002. Grizzly bear–cattle interactions on two grazing allotments in northwest Wyoming. Ursus 13:247–256.

BJORNLIE, D., AND M.A. HAROLDSON. 2002. Grizzly bear use of insect aggregation sites documented from aerial telemetry and observations. Pages 33–36 *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. Geological Survey, Bozeman, Montana, USA.

BLANCHARD, B.M., AND R.R. KNIGHT. 1995. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. Journal of Wildlife Management 59:560–565.

CRAIGHEAD, J.J., J.S. SUMNER, AND J.A. MITCHELL. 1995. The grizzly bears of Yellowstone: their ecology in the Yellowstone Ecosystem, 1959–1992. Island Press, Washington, D.C., USA.

DEBOLT, B. 2000. Feasibility of using portable electric fencing to prevent damage to livestock and apiaries by bears and other predators. Pages 122–126 *in* C.C. Schwartz and M.A. Haroldson, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2000. U.S. Geological Survey, Bozeman, Montana, USA.

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, USA.

———, M.T. BRUSCINO, S. CAIN, J. COPELAND, K. FREY, M.A. HAROLDSON, AND C.C. SCHWARTZ. 2000*a*. Grizzly bear–human conflicts, confrontations, and management actions in the Yellowstone ecosystem, 1999. Pages 55–108 *in* C.C. Schwartz and M.A. Haroldson, editors.

Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 1999. U.S. Geological Survey, Bozeman, Montana, USA.

———, M.J. BIEL, AND H.L. ROBISON. 2000*b*. Influence of vehicle speed and vegetation cover-type on road-killed wildlife in Yellowstone National Park. Pages 42–51 *in* T.A. Messmer and B. West, editors. Wildlife and highways: seeking solutions to an ecological and socio-economic dilemma. Proceedings of the 7th Annual Meeting of the Wildlife Society, Nashville, Tennessee, USA.

HAROLDSON, M.A., AND K. FREY. 2002. Grizzly bear mortalities. Pages 23–28 *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. Geological Survey, Bozeman, Montana, USA.

———, M.A. TERNENT, K.A. GUNTHER, AND C.C. SCHWARTZ. 2002. Grizzly bear denning chronology and movements in the Greater Yellowstone Ecosystem. Ursus 13:29–37.

HERRERO, S., AND A. HIGGINS. 1998. Field use of capsicum spray as a bear deterrent. Ursus 10:533–537.

HOOGE, P.N., AND B. EICHENLAUB. 1997. Animal movement extension to ArcView. Version 1.1 Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

KACHIGAN, S.K. 1982. Multivariate statistical analysis, a conceptual introduction. Radius, New York, New York, USA.

KNIGHT, R.R., AND S. JUDD. 1983. Grizzly bears that kill livestock. International Conference on Bear Research and Management 5:186–190.

———, B.M. BLANCHARD, AND L.L. EBERHARDT. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. Wildlife Society Bulletin 16: 121–125.

MATTSON, D.J. 1997. Use of ungulates by Yellowstone grizzly bears, *Ursus arctos*. Biological Conservation 81:161–177.

———. 2000. Causes and consequences of dietary differences among Yellowstone grizzly bears (*Ursus arctos*). Dissertation, University of Idaho, Moscow, Idaho, USA.

———, AND M.M. REID. 1991. Conservation of the Yellowstone grizzly bear. Conservation Biology 5:364–372.

———, C.M. GILLIN, S.A. BENSON, AND R.R. KNIGHT. 1991*a*. Bear use of alpine insect aggregations in the Yellowstone ecosystem. Canadian Journal of Zoology 69:2430–2435.

———, B.M. BLANCHARD, AND R.R. KNIGHT. 1991*b*. Food habits of Yellowstone grizzly bears, 1977–1987. Canadian Journal of Zoology 69:1619–1629.

———, B.M. BLANCHARD, AND R.R. KNIGHT. 1992. Yellowstone grizzly mortality, human habituation, and whitebark pine seed crops. Journal of Wildlife Management 56:432–442.

———, K. BARBER, R. MAW, AND R. RENKIN. 1999. Coefficients of productivity for Yellowstone's grizzly bear habitat. U.S. Geological Survey Forest and Rangeland Ecosystem Science Center, Corvallis, Oregon, USA.

MEAGHER, M., AND J.R. PHILLIPS. 1983. Restoration of natural populations of grizzly and black bears in Yellowstone National Park. International Conference on Bear Research and Management 5:152–158.

———, AND S. FOWLER. 1989. The consequences of protecting problem grizzly bears. Pages 141–144 *in* Bear–people conflicts. Proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

NELSON, R.A., G.E. FOLK, JR., E.W. PFEIFFER, J.J. CRAIGHEAD, C.J. JONKEL, AND D.L. STEIGER. 1983. Behavior, biochemistry, and hibernation in black, grizzly, and polar bears. International Conference on Bear Research and Management 5:284–290.

REINHART, D.P., AND D. MATTSON. 1990. Bear use of cutthroat trout spawning streams in Yellowstone National Park. International Conference on Bear Research and Management 8:343–350.

———, M.A. HAROLDSON, D.J. MATTSON, AND K.A. GUNTHER. 2001. Effects of exotic species on Yellowstone's grizzly bears. Western North American Naturalist 61:277–288.

SCHWARTZ, C.C., M.A. HAROLDSON, K.A. GUNTHER, AND D. MOODY. 2002. Distribution of grizzly bears in the greater Yellowstone Ecosystem, 1990–2000. Ursus 13:203–212.

STOKES, A.W. 1970. An ethologists views on managing grizzly bears. BioScience 20:1154–1157.

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.

WILKINSON, L. 1988. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois, USA.

Received: 28 May 2001
Accepted: 28 October 2003
Associate Editor: R.T. Shideler