POSSIBLE EFFECTS OF ELK HARVEST ON FALL DISTRIBUTION OF GRIZZLY BEARS IN THE GREATER YELLOWSTONE ECOSYSTEM

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Abstract: The tradition of early elk (*Cervus elaphus*) hunting seasons adjacent to Yellowstone National Park (YNP), USA, provides grizzly bears (*Ursus arctos horribilis*) with ungulate remains left by hunters. We investigated the fall (Aug–Oct) distribution of grizzly bears relative to the boundaries of YNP and the opening of September elk hunting seasons. Based on results from exact tests of conditional independence, we estimated the odds of radiomarked bears being outside YNP during the elk hunt versus before the hunt. Along the northern boundary, bears were 2.40 times more likely to be outside YNP during the hunt in good whitebark pine (*Pinus albicaulis*) seed-crop years and 2.72 times more likely in poor seed-crop years. The level of confidence associated with 1-sided confidence intervals with a lower endpoint of 1 was approximately 94% in good seed-crop years and 61% in poor years. Along the southern boundary of YNP, radiomarked bears were 2.32 times more likely to be outside the park during the hunt in good whitebark pine seed-crop years and 4.35 times more likely in poor seed-crop years. The level of confidence associated with 1-sided confidence intervals with a lower endpoint of 1 was approximately 93% in both cases. Increased seasonal bear densities and human presence in early hunt units increases potential for conflicts between bears and hunters. Numbers of reported hunting-related grizzly bear mortalities have increased in the Greater Yellowstone Ecosystem (GYE) during the last decade, and nearly half of this increase is due to bear deaths occurring in early hunt units during September. Human-caused grizzly bear mortality thresholds established by the U.S. Fish and Wildlife Service (USFWS) have not been exceeded in recent years. This is because agency actions have reduced other sources of human-caused mortalities, and because population parameters that mortality thresholds are based on have increased. Agencies must continue to monitor and manage hunter-caused grizzly bear mortality at sustainable levels to ensure the long-term health of the GYE population.

JOURNAL OF WILDLIFE MANAGEMENT 68(1):129–137

Key words: *Cervus elaphus*, elk harvest, fall distribution, Greater Yellowstone Ecosystem, grizzly bear, mortality, *Ursus arctos horribilis.*

During the 1990s, hunting-related mortalities were the single largest source of known human-caused grizzly bear deaths in the GYE (A. Dood, Montana Department of Fish, Wildlife and Parks, unpublished data). This increase in hunter-caused bear mortality has been attributed to an increasing (Eberhardt et al. 1994, Boyce et al. 2001) and expanding (Schwartz et al. 2002) bear population, which results in more frequent encounters between hunters and bears. Within the last decade, grizzly bears in the GYE have expanded their range primarily to the south and east, and an increasing number of mortalities have occurred outside of the Grizzly Bear Recovery Zone (Schwartz et al. 2002).

We suggest that another factor possibly contributing to the increased number of lethal encounters between hunters and bears is the traditional elk harvest that occurs adjacent to YNP boundaries. Ungulate harvest and wounding loss by hunters may influence the fall distribution of grizzly bears by creating dispersed "ecocenters" (Craighead et al. 1995). Grizzly bears are highly motivated to feed during the fall as they prepare to spend up to 7 months in winter dens (Haroldson et al. 2002). Bears learn to use available food resources quickly, and when food availability becomes predictable, bears establish traditional use and impart that behavior to their offspring. Availability of food associated with the elk harvest may be considered a predictable food resource to bears using areas where elk harvest is traditional. In 1986, researchers estimated that 370 tons of biomass from "gut piles" and other discarded parts was left by elk hunters annually in the GYE (Servheen et al. 1986).

Seasonally important grizzly bear foods include cutthroat trout (*Oncorhynchus clarki*; Reinhart and Mattson 1990), army cutworm moths (*Euxoa auxiliaris*; Mattson et al. 1991*a*), seeds from whitebark pine (Kendall 1983, Blanchard 1990, Matt-

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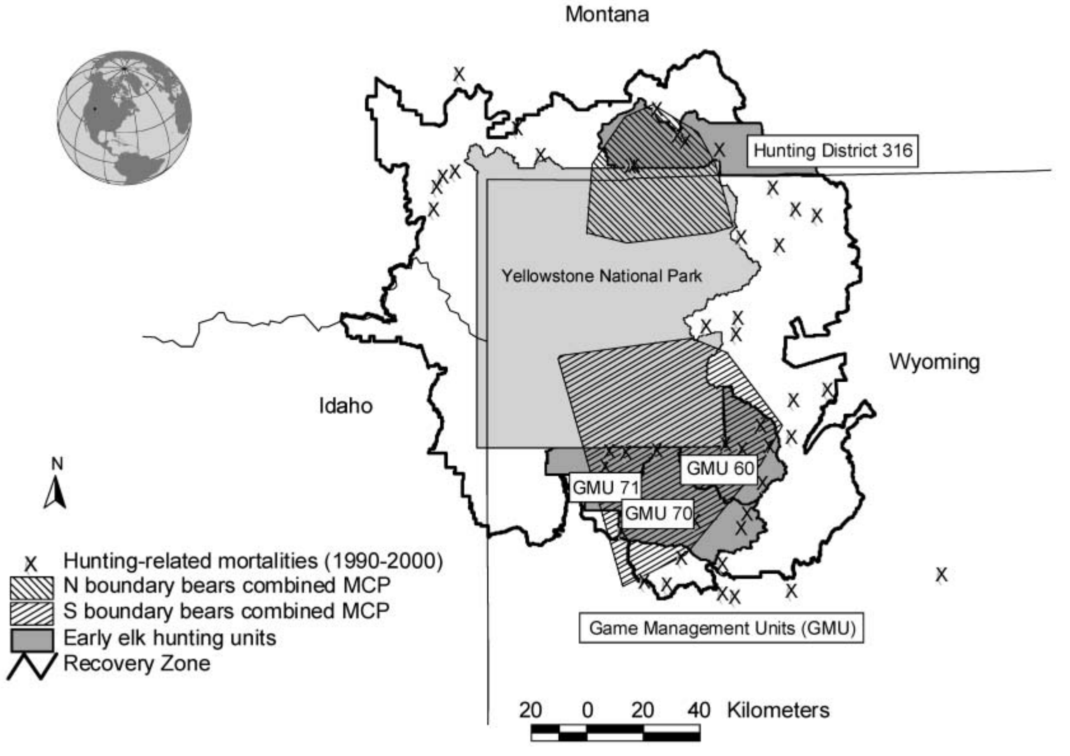

Fig. 1. Yellowstone National Park (YNP), USA, the Grizzly Bear Recovery Zone (from 1993 U.S. Fish and Wildlife Service Grizzly Bear Recovery Plan), early elk hunting unit boundaries, and location of hunting-related grizzly bear mortalities during 1990–2000. Also shown are composite minimum convex polygons (MCP) for northern (N) and southern (S) boundary bears that were investigated for changes in distribution with the opening of early elk hunting seasons.

son and Reinhart 1997), and meat from ungulates, primarily elk and bison (*Bison bison*; Mattson 1997). Recent studies using N^{15} isotopes from grizzly bear hair suggest that in the GYE grizzly bears obtain much more of their annual energy requirements from meat than do other interior grizzly populations examined (Hilderbrand et al. 1999). Meat constitutes as much as 79 and 45% of the annual diet for males and females, respectively, in the GYE (Jacoby et al. 1999). An inverse relationship between annual fall whitebark pine seed crops and human-caused grizzly bear mortality has been demonstrated (Mattson et al. 1992). Meat from ungulates becomes more important during years with poor whitebark pine cone crops (Mattson 1997, Felicetti et al. 2003).

We investigated the distribution of radiomarked bears that lived near either the northern or southern boundaries of YNP prior to and during early elk hunting seasons. Our working hypotheses was that grizzly bears spend more time outside YNP during the early hunting seasons, and that this increased use is due to the availability of ungulate remains left by hunters. Search for and use of whitebark pine seeds outside YNP was the alternative hypothesis we examined.

STUDY AREA

The GYE encompasses approximately 37,000 km^2 in the states of Wyoming, Montana, and Idaho, USA, and encompasses YNP and portions of 6 national forests that surround the park (Fig. 1). Detailed descriptions of the GYE can be found in Knight and Eberhardt (1985), Blanchard and Knight (1991), Mattson et al. (1991*b*), and Schwartz et al. (2002).

Early rifle hunting seasons for elk occurred in wilderness settings both north and south of YNP during September. The Montana early elk hunt extends from 15 September to 26 November in Hunting District 316 (Fig. 1), 5 weeks earlier than the general rifle season for elk in other Montana hunting districts adjacent to YNP. Most of Hunting District 316 occurs within the Absaroka-

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Table 1. Counts of trees above and below the overall median cone production (3 cones/tree) on whitebark pine transects during years with location data for radiomarked grizzly bears along the northern and southern boundary of Yellowstone National Park, USA. Years were considered "good" when the majority of trees contained >3 cones/tree and "poor" when most trees contained ≤3 cones/tree. We obtained no fall grizzly bear locations associated with either the northern or southern boundary during 1993.

	Year										
	1989	1990	1991	1992	1994	1995	1996	1997	1998	1999	2000
No. trees > median cones	182	16	125	136	19	25	159	43	102	157	48
No. trees ≤ median cones	27	191	52	51	159	163	29	145	85	30	128
Rating	Good	Poor	Good	Good	Poor	Poor	Good	Poor	Good	Good	Poor

Beartooth Wilderness of the Gallatin National Forest. The Wyoming early rifle hunt for elk begins 10 September in Game Management Unit (GMU) 60 and generally closes the third week in October. Elk rifle seasons begin 1 and 2 weeks later in GMUs 70 and 71 and run through 31 October and 15 November, respectively. Wyoming GMUs occur predominantly within the Bridger-Teton Wilderness of the Bridger-Teton National Forest (Fig. 1). Grizzly bears within the GYE have not been legally hunted since 1974. Early elk hunts have occurred in Montana and Wyoming since before 1966 and 1934, respectively, but we were unable to find records to determine the exact years.

METHODS

We used radiotelemetry to investigate grizzly bear distribution relative to elk-harvest seasons adjacent to YNP during mid-September in both Montana and Wyoming. Most grizzly bears captured were radiomarked with the exception of dependent offspring (cubs or yearlings). We typically fitted adult bears with radiocollars (Telonics, Inc., Mesa, Arizona, USA) with breakaway canvas inserts. Independent subadult bears were instrumented with expandable collars (Blanchard 1985), glue-on-hair transmitters, or ear-tag transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA). Weather permitting, we conducted radiotracking flights to locate radiomarked bears weekly from mid-April through November.

We used radio locations of nontransport-influenced bears only (i.e., bears not relocated because of nuisance activity) obtained from 1 August through 1 November, 1983–2000. We used post-1982 data because 1983 is considered the year when intensive management began in an effort to reduce bear mortalities and is approximately 1 bear generation after cessation of legal grizzly bear hunting in the GYE. We assumed that this period allowed sufficient time for a tradition of gut pile use to develop. Data from 239 bears with 4,248 locations were available. From these data, we selected those individuals that were located both inside and outside YNP during the specified period (70 individuals with 966 locations). We then selected bears located within 5 km of the northern or southern boundary of YNP in units with an early elk season. We included only bears located during both prehunt and hunting periods. This resulted in a sample of 19 bears with 307 locations from 1989–2000, excluding 1993.

We defined the prehunt period as 1 August–14 September (45 days) and the hunting period as 15 September–1 November (46 days) for northern-boundary bears. Prehunt for southern-boundary bears was 1 August–9 September (40 days), and hunt was 10 September–1 November (51 days). Actual hunting seasons in both Montana and Wyoming extended well past 1 November, but we chose to curtail the analysis at 1 November to compare periods of similar duration.

We used results from 19 whitebark pine cone production transects (Blanchard 1990) conducted annually from 1980–2000 to rate cone production. Years with most trees producing cones below the overall median were considered poor cone-producing years. Years with most trees above the overall median were considered good (Table 1).

We analyzed movements of bears on the northern and southern boundaries of YNP in good and poor whitebark pine seed-crop years. We hereafter refer to these scenarios as NG (Northern boundary–Good year), SG (Southern boundary–Good year), NP (Northern boundary–Poor year), and SP (Southern boundary–Poor year). We examined the association between period (prehunt, hunt) and location of observations (inside YNP, outside YNP) while controlling for individual bear effects. Our analysis consisted of using exact inference procedures to estimate odds ratios in 3-way (period, location, individual) contingency tables (Agresti 1990). The test pro-

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cedure was conditioned on fixed-strata marginal totals and was an exact small-sample alternative to the Cochran-Mantel-Haenzel test (Agresti 1990:232). Our null hypothesis was that the common odds ratio equaled 1; the alternative hypothesis was that the odds ratio was >1. We were more interested in estimating the common odds ratios for each of the 4 scenarios. We also determined the confidence level associated with the lower 1-sided interval (1, ∞). The intervals provided an assessment of how confident we were that bear movements were more likely to be outside YNP during the hunt than prior to the hunt.

The exact conditional tests of independence were carried out on 4 2 $\leftrightarrow$ 2 $\leftrightarrow$ K contingency tables, where K indicates the number of bears. We used 1 table for each of the 4 boundary–whitebark pine combinations with the following sample sizes: NG: 90 observations on 7 bears; NP: 19 observations on 3 bears; SG: 127 observations on 8 bears; and SP: 71 observations on 7 bears. The total number of bears exceeded 19 because some individuals occurred in >1 scenario.

A key assumption was that individual bears share a common odds ratio. We evaluated this by fitting the log-linear model corresponding to this assumption and comparing fitted tables with observed tables by plotting fitted values against observed values. We did not use log-linear models for the analysis because inference in such models is based on large sample sizes, but the plots allowed for a visual assessment of the reasonability of the common odds ratio assumption.

We used the 1998 Geographic Information System (GIS) vegetation layer developed for the Yellowstone Cumulative Effects Model (R. Maw, U.S. Forest Service, personal communication) to assess the availability of whitebark pine cover types. Composite minimum convex polygons (MCP) constructed from north-boundary bear locations and south-boundary locations were used to delineate the extent of fall use by these bears (Fig. 1). Each MCP polygon was populated with 2,000 random points. We estimated availability of whitebark pine cover types by intersecting random points with whitebark pine stands delineated within the GIS vegetation layer. Bear association with whitebark pine was estimated via the same procedure except we used presence of whitebark pine stands within a 250-m radius, which was consistent with estimates of aerial telemetry error. We also investigated presence of whitebark pine stands within 1,300 m of bear locations. This distance approximates the average daily activity radius for adult female grizzly bears in the GYE. We assessed differences in availability and use (within 250 m and 1,300 m) of whitebark pine stands relative to YNP boundaries and opening of the early elk hunting seasons using chi-square tests.

We also investigated hunting-related grizzly bear mortalities documented between 1983 and 2000. We defined hunting-related mortalities as incidents that resulted in bear deaths directly related to the pursuit of legal game. These primarily included chance encounters between bears and hunters in the field, conflicts over ungulate carcasses, and conflicts at hunter camps, often related to game meat in camps. We obtained specific information regarding mortalities from the Montana Department of Fish, Wildlife, and Parks (A. Dood, Montana Department of Fish, Wildlife, and Parks, unpublished data), which maintains the grizzly bear mortality database for the GYE. The degree of certainty associated with each record in the mortality database is classified as (1) known, where carcasses were recovered or other evidence to indicate known status was available; (2) probable, where strong evidence to indicate a mortality had occurred but no carcass was recovered; and (3) possible, where some presumptive evidence of a mortality existed but no prospects for validation were found (Craighead et al. 1988). We used ArcView (Environmental Systems Research Institute 1992) shapefiles for hunting unit boundaries, obtained from each state wildlife management agency, to identify hunter-related mortalities occurring within these areas.

We conducted our analysis using the R statistical programming language (Version 1.6.1), which is freeware similar to Splus (MathSoft, Inc., Seattle, Washington, USA) and can be downloaded at http://cran.us.r-project.org. Spatial analyses were conducted using ArcView with Spatial Analyst (Environmental Systems Research Institute 1992) and the Animal Movement Extension (Hooge and Eichenlaub 1997).

RESULTS

Results of annual whitebark pine cone surveys indicated that median cone production was 3 cones/tree during 1989–2000 (Table 1). Rating annual cone production relative to the median resulted in “good” ratings during 6 years and “poor” ratings during 5 years that we had bear locations. No fall grizzly bear locations associated with either the northern or southern boundary

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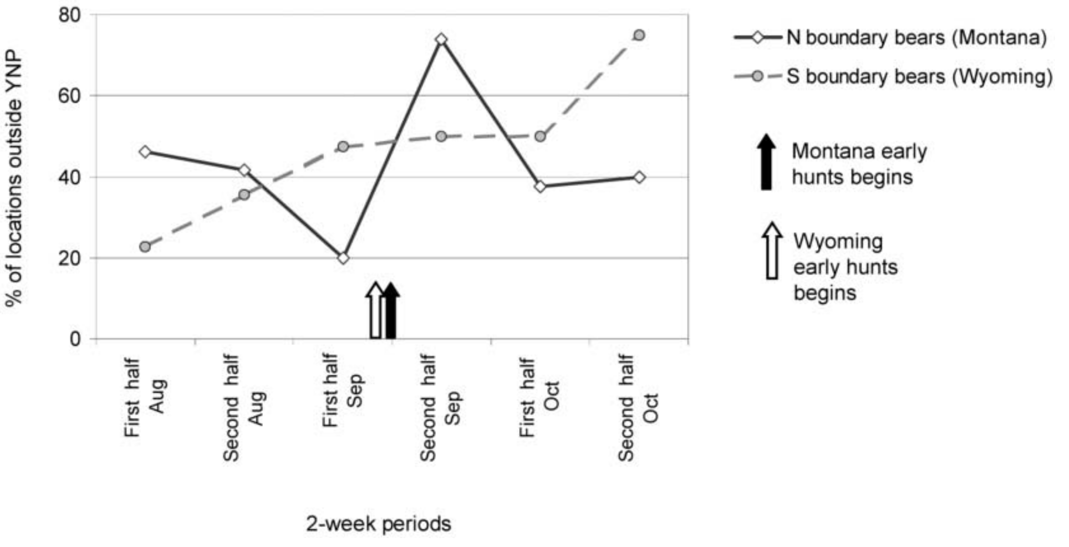

Fig. 2. Proportion of northern (N; in Montana [MT]) and southern (S; in Wyoming [WY]) boundary radiomarked grizzly bears outside Yellowstone National Park (YNP), USA, during August through October 1989–2000, excluding 1993 when no fall locations associated with either boundary were obtained. Early elk rifle seasons began at the start of the second half of September along the northern boundary to YNP, and near the end of the first half of September along the southern boundary.

of YNP were obtained in 1993.

Distribution of bear locations outside YNP along the northern boundary changed abruptly and correlated with the opening of the elk hunting season (Fig. 2). Change in distribution of bear locations outside YNP along the southern boundary was less abrupt, but the percent of bears outside YNP increased throughout the hunting period (Fig. 2).

We estimated that the common odds ratio exceeded 2 in all 4 scenarios. Along the northern boundary, bears were 2.40 and 2.72 times more likely to be outside the YNP during the hunt during NG and NP, respectively. Along the southern boundary, bears were 2.32 and 4.35 times more likely to be outside YNP during SG and SP, respectively. Our levels of confidence that the true common odds ratio exceeded 1 were 94% (NG), 61% (NP), 93% (SG), and 93% (SP) of the time. The low level of confidence associated with NP was due to the small sample size (19 observations on 3 bears) for that scenario. Our evaluation of the reasonableness of our common odds ratio assumption indicated no problems.

Our assessment of whitebark pine distribution in the combined MCP along the northern boundary indicated significantly more whitebark pine stands outside (18%) than inside (11%) YNP (n = 2,000, χ^2 = 17.199, df = 1, $P < 0.001$). However, we observed no significant difference (n = 109, χ^2 = 0.168, df = 1, P = 0.682) in number of bear locations within 250 m of whitebark stands inside (46.0%) versus outside (50.0%) YNP, or between (n = 109, χ^2 = 0.012, df = 1, P = 0.913) the prehunt (47.2%) and the hunting (48.2%) periods. In the combined MCP along the southern boundary, we found significantly more whitebark pine inside (16.6%) than outside (13.4%) YNP (n = 1,950, χ^2 = 3.854, df = 1, P = 0.05). We observed no difference (n = 198, χ^2 = 0.358, df = 1, P = 0.549) in frequency of bear locations within 250 m of whitebark pine stands between the prehunt (59.5%) and hunt (55.3%) periods. However, bear locations outside YNP (45.1%) were not closely associated with whitebark pine stands (within 250 m) as often as were locations inside (67.3%) YNP (n = 198, χ^2 = 9.923, df = 1, P = 0.002).

We found no significant differences when we compared the presence of whitebark pine stands within 1,300 m of bear locations between the prehunt and hunt periods, and inside versus outside YNP. Of interest was the result that 78.0% of bear locations associated with the northern boundary occurred within 1,300 m of whitebark pine stands; compared to only 61.0% of random points. Similarly 82.8% of the southern-boundary bear locations were within 1,300 m of whitebark pine stands; compared to only 60.3% of ran-

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dom points.

DISCUSSION

The opening dates of the Montana early rifle seasons for elk have been relatively consistent over the years, occurring in mid-September. During typical years, most of the hunter harvest occurs during the first week of the season (K. Frey, Montana Department of Fish, Wildlife, and Parks, personal communication). Bears feeding on gut piles would maximize their success by moving outside YNP coincident with the first 2 weeks of the hunting season. Timing of change in distribution of radiomarked bears associated with the northern boundary to YNP was most pronounced during the first 2 weeks of the hunting seasons. In contrast, opening dates for Wyoming hunting units adjacent to the southern boundary of YNP varied by 1–2 weeks. Also, a sequence of opening dates for different ungulate species occurred from early to mid-September, and the harvest was not compressed into the first weeks of the season, as was the case in Montana. These factors explain the increased frequency of radiomarked grizzly bear locations outside YNP throughout the hunting period observed in Wyoming.

Shifts in the distribution of our radiomarked bears were undoubtedly resource related. August through October coincides with hyperphagia (Nelson et al. 1983) in grizzly bears. During this period, bears focus on fattening in preparation for winter hibernation. Given the season, timing of shifts in bear distribution, and area of use, we believe that our analyses supports the hypothesis that grizzly bears spend more time outside YNP during the early hunting seasons and that this increased use is due to the availability of ungulate remains left by hunters. Our results clearly demonstrate that bears were at least 2 times as likely to be outside YNP during the hunt than prior to the hunt. This movement occurred regardless of good versus poor whitebark pine seed production. The consistent presence of whitebark pine stands within a daily activity radius of bear locations also suggests that bears could be using areas that would maximize the potential for finding either elk remains left by hunters or red squirrel (*Tamiasciurus hudsonicus*) middens containing whitebark pine cones.

Assuming that the observed shift in the distribution of radiomarked bears reflects the distribution of unmarked bears, one could anticipate a seasonally high concentration (dispersed ecocenter) of grizzly bears associated with the early elk hunt. This shift creates a situation in which large numbers of grizzly bears are in close association with large numbers of armed humans during a season when bears are driven to forage. During recent years, anecdotal descriptions from outfitters, guides, and hunters from both the northern and southern areas indicate that encounters between humans and bears are a common occurrence during the early hunting season. Two decades ago, many of these same outfitters and guides considered observations of grizzly bears a rare event.

Estimates of hunter numbers in the Yellowstone Grizzly Bear Recovery Zone were constant or declined during the 1990s (Moody et al. 2002), while the number of hunting-related grizzly bear mortalities increased in the GYE (Fig. 3). Much of this increase can be attributed to incidents that occurred during the early elk harvest units in Montana and Wyoming (Fig. 4). During 1996–2000, more than half (56%, $n = 28$) of the known and probable hunting-related mortalities occurred because of chance encounters between bears and hunters in pursuit of game (M. Bruscino, Wyoming Game and Fish Department, personal communication). Conflicts between bears and humans over carcasses and/or in backcountry camps account for the remaining mortalities. In a portion of Montana Hunting District 316 during 2000, the number of backcountry camps increased from <10 per week prior to the opening of the hunting season to a high of 90 camps during the opening week of hunting season (Ruth et al. in press). Although we lack similar information for the southern-boundary area, we suspect that similar increases in the number of camps occurred.

Approximately 2 bear generations have passed since legal hunting stopped and grizzly bears in the GYE were given protected status. During this time, the long-standing tradition of early elk harvest seasons adjacent to YNP has provided considerable food resources to bears (Servheen et al. 1986), with presumably little negative impact (for bears not killed in conflicts) from increasing familiarization with humans. Because bears learn quickly (Bacon and Burghardt 1976) and females pass on learned behaviors to their offspring (Jonkel 1978, Gilbert 1989, Meagher and Fowler 1989), 2 generations seems ample time and the motivation exists for a pattern of traditional use to be expressed. Our observations are not unique, since hunter harvest of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) and elk correspond with increased hunting-related mortalities

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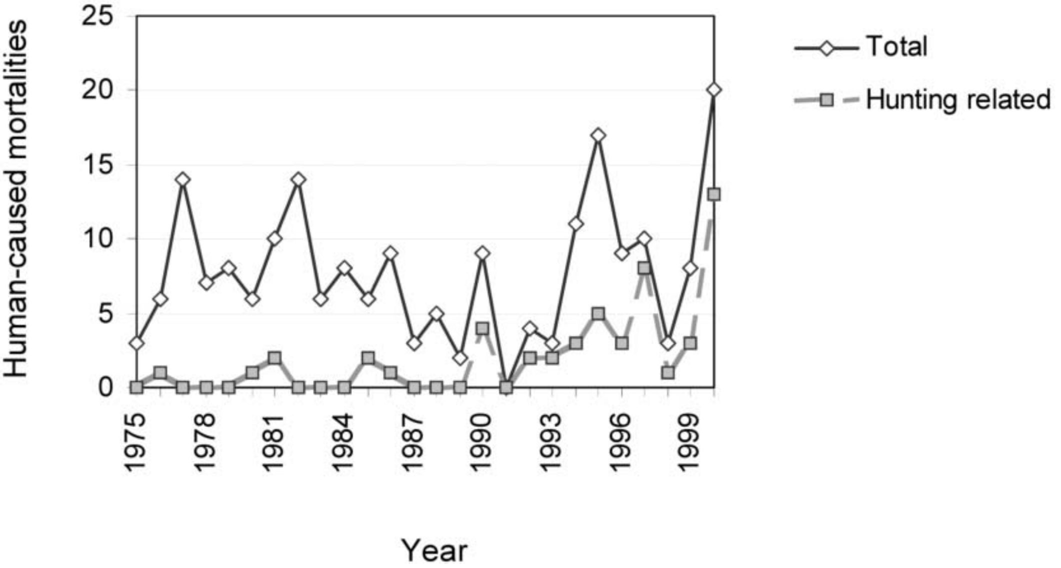

Fig. 3. Documented known and probable human-caused grizzly bear mortalities and numbers of hunting-related grizzly bear mortalities during 1975–2000 in the Greater Yellowstone Ecosystem, USA.

MANAGEMENT IMPLICATIONS

of brown bears on Kodiak and Admiralty Islands, Alaska, USA (Smith et al. 1989, Barnes 1994).

The management implications of our findings are clear. Early elk hunting seasons have created a reliable and highly nutritious source of food for grizzly bears during the fall when bears are actively foraging and preparing for hibernation. Bears leave the protection of YNP and move into close proximity to hunters, which can result in dead bears. At issue is the number of bear mortalities and the consequences to long-term health of the bear population. While the recent increase in hunter-related grizzly bear mortalities is cause for

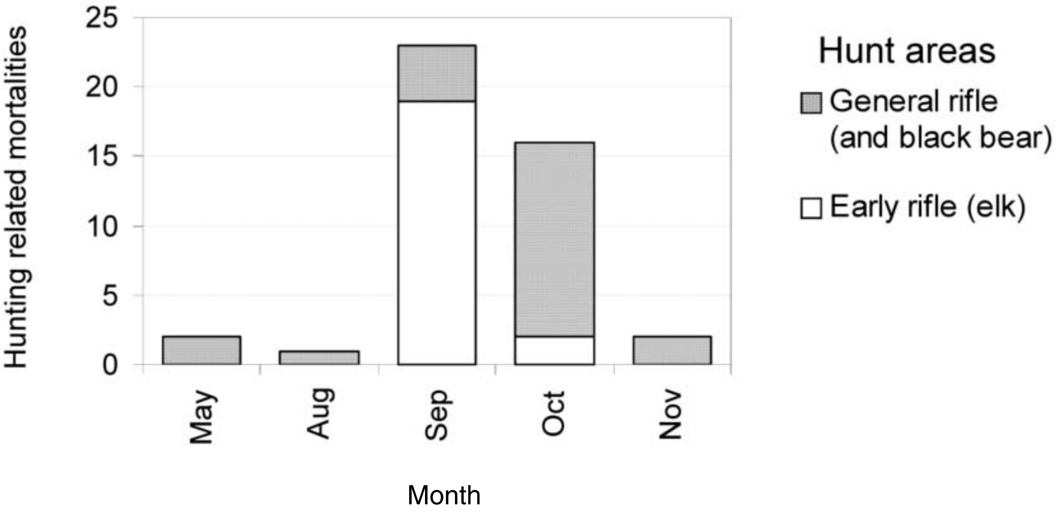

Fig. 4. Numbers of reported known and probable hunting-related grizzly bear mortalities occurring in early elk hunting units and other areas by month during 1990–2000 in the Greater Yellowstone Ecosystem, USA. Grizzly bear mortalities occurring during May and August were the result of mistaken identity during legal black bear hunting seasons.

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concern, total human-caused mortality limits established in the Grizzly Bear Recovery Plan (U.S. Fish and Wildlife Service 1993) have not been exceeded in recent years (Haroldson and Frey 2001). This is due to an increase in minimum population estimates and a decline in other sources of human-caused bear mortalities such as management removals due to livestock depredation or nuisance activity in human developments.

Keeping human-caused grizzly bear mortality at or below sustainable limits of population size is a critical component of grizzly bear conservation. If hunter-related mortalities continue to increase and/or if hunter-related mortalities go undetected (i.e., unreported), the current health of the GYE grizzly bear population could change. Such concerns have prompted managers (Yellowstone Ecosystem Subcommittee) to establish a working group including agencies, outfitters, environmental groups, and other concerned individuals to identify, prioritize, and make management recommendations to address these issues. Management recommendations likely will include a focus on increased education of hunters, guides, and outfitters to reduce hunter–bear encounters. Guidelines could include immediate removal of edible portions of harvested elk from the kill site, minimal (i.e., short-duration) storage of meat in the backcountry, elimination of any meat processing in and around campsites, and the use of 2-way communication between hunters and guides to reduce the time a harvested animal is unattended. With proper management and continued vigilance on the part of agencies and the public, we can ensure the long-term health of the GYE grizzly bear and retain the long tradition of consumptive harvest of elk adjacent to YNP.

ACKNOWLEDGMENTS

We acknowledge the pilots who have flown grizzly bear radiotracking flights in the GYE for many years: D. Stradley, R. Stradley, S. Monger, G. Lust, R. Hyatt, J. Spencer, S. Rasmussen, and C. Tyrrel. Personnel who were primarily responsible for trapping and collaring bears included J. Jonkel, K. Inberg (deceased), B. Schleyer, C. Dickinson, M. Lamoreux, M. Ternent, G. Holms, and C. Anderson. We also recognize D. Tyers and K. Frey for discussions that contributed to formalizing ideas for this paper. M. Bruscino and K. Frey provided information on grizzly bear mortalities. A pilot study conducted by The Northern Range Large Carnivore Working Group, specifically T. Ruth and D. Smith, also provided insights. We presented preliminary results of this work to a Statistical Consulting class taught by J. Borkowski, Math Department, Montana State University, during fall semester 2001. Insights obtained from classroom discussions significantly influenced our analytical approach. We also thank K. West and C. Costello for editing early drafts of the manuscript.

LITERATURE CITED

AGRESTI, A. 1990. Categorical data analysis. John Wiley & Sons, New York, New York, USA.

BACON, E. S., AND G. M. BURGHARDT. 1976. Learning and color discrimination in the American black bear. International Conference on Bear Research and Management 3:27–36.

BARNES, V. G., JR. 1994. Brown bear–human interactions associated with deer hunting on Kodiak Island. International Conference on Bear Research and Management 9(1):63–73.

BLANCHARD, B. 1985. Field techniques used in the study of grizzly bears. Interagency Grizzly Bear Study Team Report, Bozeman, Montana, USA.

———. 1990. Relationship between whitebark pine cone production and fall grizzly bear movements. Pages 362–363 *in* W. C. Schmidt and K. J. McDonald, editors. Proceedings of symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. U.S. Forest Service General Technical Report INT-270. U.S. Forest Service, Ogden, Utah, USA.

———, AND R. R. KNIGHT. 1991. Movements of Yellowstone grizzly bears, 1975–87. Biological Conservation 58:41–67.

BOYCE, M. S., B. M. BLANCHARD, R. R. KNIGHT, AND C. SERVHEEN. 2001. Population viability for grizzly bears: a critical review. International Association for Bear Research and Management, Monograph Series 4.

CRAIGHEAD, F. C., J. S. SUMNER, AND J. A. MITCHELL. 1995. The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959–1992. Island Press, Covelo, California, USA.

CRAIGHEAD, J. J., K. R. GREER, R. R. KNIGHT, AND H. I. PAC. 1988. Grizzly bear mortalities in the Yellowstone Ecosystem, 1959–1987. Report of the Montana Department of Fish, Wildlife, and Parks; Craighead Wildlife Institute; Interagency Grizzly Bear Study Team; and National Fish and Wildlife Foundation.

EBERHARDT, L. L., B. M. BLANCHARD, AND R. R. KNIGHT. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology 72:360–363.

ENVIRONMENTAL SYSTEMS RESEARCH INSITUTE. 1992. ArcView GIS. Version 3.2. Environmental Systems Research Institute, Redlands, California, USA.

FELICETTI, L. A., C. C. SCHWARTZ, R. O. RYE, M. A. HAROLDSON, K. A. GUNTHER, AND C. T. ROBBINS. 2003. Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. Canadian Journal of Zoology 81:763–770.

GILBERT, B. K. 1989. Behavioral plasticity and bear human conflicts. Pages 1–8 *in* M. Bromley, editor. Bear–people conflicts: proceedings of a symposium

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on management strategies. Yellowknife, Northwest Territories, Canada.

HAROLDSON, M. A., AND K. FREY. 2001. Grizzly bear mortality. Pages 24–27 *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.

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

HILDERBRAND, G. V., C. C. SCHWARTZ, C. T. ROBBINS, M. E. JACOBY, T. A. HANLEY, S. M. ARTHUR, AND C. SERVHEEN. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal Zoology 77:132–138.

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.

JACOBY, M. E., G. V. HILDERBRAND, C. SERVHEEN, C. C. SCHWARTZ, S. M. ARTHUR, T. A. HANLEY, C. C. ROBBINS, AND R. MICHENER. 1999. Trophic relations of brown and black bears in several western North American ecosystems. Journal of Wildlife Management 63:921–929.

JONKEL, C. J. 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. Wildlife Management Institute. Stackpole Books, Harrisburg, Pennsylvania, USA.

KENDALL, K. C. 1983. Use of pine nuts by grizzly and black bears in the Yellowstone area. International Conference on Bear Research and Management 5:166–173.

KNIGHT, R. R., AND L. L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:323–334.

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*b*. Food habits of Yellowstone grizzly bears, 1977–87. Canadian Journal of Zoology 69:1619–1629.

———, ———, AND ———. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. Journal Wildlife Management 56:432–442.

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

———, 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.

MEAGHER, M., AND S. FOWLER. 1989. The consequence of protecting problem bears. Pages 141–144 *in* M. Bromley, editor. Bear–people conflicts: proceedings of a symposium on management strategies. Yellowknife, Northwest Territories, Canada.

MOODY, D., L. HANAUSKA-BROWN, AND K. ALT. 2002. Trends in elk hunter numbers within the Grizzly Bear Recovery Zone plus the 10-mile perimeter area. Pages 51–52 *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.

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

RUTH, T. E., D. W. SMITH, M. A. HAROLDSON, P. C. BUOTTE, C. C. SCHWARTZ, H. B. QUIGLEY, S. CHERRY, D. TYERS, AND K. FREY. In press. Response by three large carnivores to recreational big game hunting along the Yellowstone National Park and Absaroka–Beartooth Wilderness boundary. Wildlife Society Bulletin.

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

SERVHEEN, C., R. KNIGHT, D. MATTSON, S. MEALEY, D. STRICKLAND, J. VARLEY, AND J. WEAVER. 1986. Report to the Interagency Grizzly Bear Committee on the availability of foods for grizzly bears in the Yellowstone ecosystem. Missoula, Montana, USA.

SMITH, R. B., V. G. BARNES, JR., AND L. J. VAN DAELE. 1989. Brown bear-human conflicts in the Kodiak Archipelago, Alaska. Pages 111–119 *in* M. Bromley, editor. Bear–people conflicts: proceedings of a symposium on management strategies. Yellowknife, Northwest Territories, Canada.

U.S. FISH AND WILDLIFE SERVICE. 1993. Grizzly bear recovery plan. Missoula, Montana, USA.

FWS_LIT_004912