GRIZZLY BEAR–CATTLE INTERACTIONS ON TWO GRAZING ALLOTMENTS IN NORTHWEST WYOMING

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Abstract: We determined cause of death for 182 cattle found dead on 2 adjacent public land grazing allotments in northwest Wyoming during 1994–96. Grizzly bears (*Ursus arctos*) killed fifty-one calves and 6 adults, representing 1.1% (mean) of the annual calf herd and 0.1% of the annual adult herd. An additional 0.9–1.8% of remaining calves were missing each year. Black bears (*U. americanus*), although present, were not implicated in cattle depredation. We believe that missing calves experienced depredation similar to discovered calves because the proportion killed by bears was similar for those equipped with mortality-sensing transmitters and unmarked calves ($P = 0.73$). Thus, estimated depredation equaled 78 calves or 1.3–2.2% of the annual calf herd. All observed depredation occurred at night ($n = 9$). Kills were separated by a mean of 3 days ($n = 50$) and occurred between 16 June and 13 September (median = 9 August). Radiotagged grizzly bears ($n = 17$) spent a greater proportion of time in the study area while depredations were occurring, and 10 were located near cattle more frequently than expected ($P < 0.05$), but most did not kill cattle. Although individuals from all sex and age (subadult, adult) groups except subadult males killed cattle, 3 adult males were responsible for 90% of confirmed losses. We employed management actions including euthanasia, translocation, and aversive conditioning to remove chronic depredators. No depredations were discovered following absence of the 3 depredating males in 1996, unlike the previous 2 years when losses continued for an additional 4 to 6 weeks. This suggests that removal of chronic depredators can reduce losses. Other bears did not become more depredatory, although many were known to utilize cattle carcasses. Removal of cattle carcasses during 1996 appeared to reduce bear densities but did not deter depredatory bear behavior. Identification and removal of depredatory individuals appears key in addressing conflicts with grizzly bears on rangelands.

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Conflicts between grizzly bears and cattle have increased in the Yellowstone Ecosystem during the last decade (Gunther et al. 1999). Bear numbers appear to have increased during this time (Eberhardt et al. 1994, Boyce 1995, Eberhardt and Knight 1996). Burgeoning bear problems increase workloads and financial anxiety for wildlife managers and livestock owners, although most importantly they reduce tolerance by the local public of bears and their range expansion. Public support for grizzly bear expansion may diminish if livestock conflicts continue to increase, which is likely in northwest Wyoming because most areas suitable for bear expansion contain livestock (Wyoming Game and Fish Department 2001).

A better understanding of bear–livestock interactions may alleviate some concerns and reduce losses, increasing support for bears. Several studies confirmed that bears kill domestic sheep (Mysterud 1980, Elgmork 1982, Johnson and Griffel 1982, Camarra 1986), arguing that sheep and grizzly bears are incompatible on the same range in some situations (Knight and Judd 1983, Sagor et al. 1997), but studies of cattle depredation are less conclusive. For example, Knight and Judd (1983) reported that bears rarely killed cattle when they coexisted around Yellowstone National Park, and Claar et al. (1986) proposed that most grizzlies were not cattle depredators. Conversely, cases of frequent depredations were documented in European bear populations with much lower bear densities than Yellowstone National Park (Clevenger et al. 1994) and in areas with much higher bear densities such as Kodiak Island (Eide 1965). Thus, uncertainty about cattle–bear interactions remains and has prevented wildlife managers from determining the best response in many cases.

Murie (1948), studying grizzly bears in the Blackrock and Spread Creek drainages of northwest Wyoming, speculated that removing specific individuals caught killing cattle may successfully limit cattle losses while maintaining viable bear populations. He also suspected, however, that most grizzlies preyed upon cattle, which could inhibit success of selective removal.

Seasonal grazing by domestic cattle and horses has occurred since 1912 in the Blackrock–Spread Creek Area (BSA) studied by Murie (1948). Accurate records of annual cattle losses on BSA have been documented since 1985 (Walton Ranch, Jackson, Wyoming, USA). During 1985–91, annual calf losses averaged 2.5% of calves grazed on BSA. None of the calves found dead during this period was reported as bear depredation. In 1992, 6

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of 18 calves examined were confirmed as grizzly bear kills, but total losses remained similar to 1985–91 (2.7%). In 1993, the proportion of calves lost increased to 12.4% and bear-killed carcasses became common (25 confirmed). We investigated grizzly bear–cattle interactions from 1994–96 to identify the reason for this intensifying problem and to examine potential solutions. Our objectives were to investigate (1) the extent of cattle losses attributable to bears, (2) the number and proportion of bears using the area and killing cattle, (3) the effect of lethal and non-lethal management actions on reducing problems, and (4) the implications for recovery of the threatened Yellowstone grizzly bear population.

STUDY AREA

Our 448 km^2 study area consisted of mountainous topography in northwest Wyoming and encompassed 2 adjacent public land grazing allotments (Fig. 1), including Blackrock–Spread Creek (BSA; Bridger-Teton National Forest) and Elk Ranch East (ERA; Grand Teton National Park). Both were managed by their respective agencies as multiple-use areas and contained numerous forest roads and trails. Dominant vegetation types included spruce–fir forests (*Picea engelmannii*, *Abies lasiocarpa*, *Pseudotsuga menziesii*), whitebark pine (*Pinus albicaulis*), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), big sagebrush (*Artemisia tridentata*)–grass–forb meadows, and willow (*Salix* spp.) riparian. Habitat type composition was 36% sagebrush grasslands, 28% lodgepole pine, 25% spruce–fir–whitebark pine, 8% clear cut, 2% aspen, and 1% willow riparian (Holm 1998). Irrigated pastures covered much of the ERA. Elevation varied from 2,050 m to 3,145 m, west to east, and annual precipitation during June–September averaged 12.4 cm.

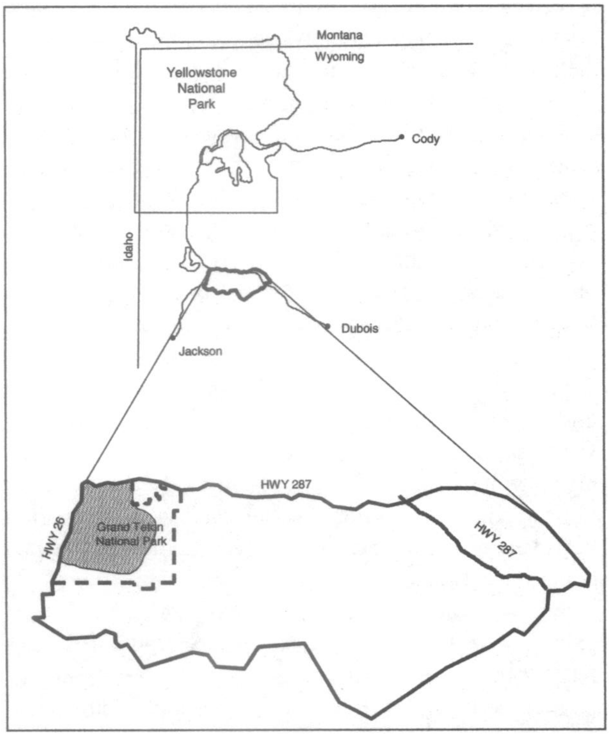

Fig. 1. Study area map of the Elk Ranch East cattle allotment (hatched area) in Grand Teton National Park (dashed line) and the Blackrock–Spread Creek cattle allotment in Bridger-Teton National Forest (area outside Grand Teton National Park), northwest Wyoming.

Approximately 900 domestic cow–calf pairs grazed annually on ERA from early July to late October. These cattle dispersed little and were managed on a rest–rotation grazing system in pastures occupying the west end of the study area (Fig. 1). On BSA, approximately 750 cow–calf pairs, 40 bulls, and <30 yearlings grazed annually between early June and mid-October. These cattle moved gradually through the allotment from west to east, arriving on the eastern end of the allotment in late July and returning west in early September (Fig. 1).

METHODS

We captured grizzly bears with Aldrich foot snares and culvert traps baited with ungulate or cattle carcasses (Jonkel 1993). Traps were distributed throughout the study area beginning at lower elevations in June and progressing upslope with seasonal snow melt. To minimize time captured animals were in traps, no more than 12 trap-sites were maintained daily. We immobilized captured bears with tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Aveco Company Incorporated, Cherry Hill, New Jersey, USA). Each bear was ear-tagged, and individuals >1 year-old were fitted with radiocollars or backpack transmitters (Telonics Incorporated, Mesa, Arizona, USA). Black bears were also radiotagged and monitored for a concurrent study (Holm et al. 1999).

We located radio-equipped bears every night (0000–0600 hrs) and occasionally during daylight hours while cattle occupied the study area. Locations in universal transverse Mercator (UTM) coordinates were determined from telemetry bearings using XYLOG plotting software (Dodge and Steiner 1986). We collected telemetry bearings using hand-held 2-element antennas, stationary null-peak towers with 8-element Yagi antennas, and truck-mounted masts with null-peak 3-element antennas (Holm 1998). We reported residency rates (percent use) for individual bears as the number of locations on the study area (1/day) divided by total number of days each bear was monitored. Radiotagged bears that left the study area were monitored every 4–7 days from fixed-wing aircraft, but location data were not included in analyses.

We mapped the distribution of cattle each morning by driving and searching for cattle in 35 survey blocks encompassing the study area. Block size varied (6.3–23.8 km^2) depending on access and our ability to detect cattle. Blocks without cattle were recorded as unoccupied, and block occupancy was assigned regardless of cattle density. Bear presence in blocks was determined by overlaying telemetry locations. We tested for spatial association (Ludwig and Reynolds 1988) between individual bears and cattle using χ^2 contingency analyses (Zar 1984) excluding days when the tested bear was absent from the study area; we constructed 2 x 2 tables representing number of blocks where only cattle occurred, number of blocks where only the bear occurred, number of blocks where both occurred, and number of blocks where neither the bear or cattle occurred. We considered all statistical tests significant at $P < 0.05$ using a Pearson χ^2 statistic unless fitted values fell below 5, in which case Fisher's exact test was used (SYSTAT statistical package, version 9.01, SPSS Incorporated, Chicago, Illinois, USA). Association probabilities and residency rates were calculated while depredations were occurring (depredation period) and absent (non-depredation period). Depredation periods were defined as the interval between first and last documented bear depredation each year; data from all 3 years were pooled for each bear.

We necropsied all dead cattle we discovered to determine cause of death (bear or other). Three people, 2 on BSA and 1 on ERA, were employed full-time by cattle owners to care for livestock and report mortalities. They typically traversed cattle-occupied areas daily from horseback or vehicle. Study personnel also searched for mortalities daily and investigated any potential signs (e.g., congregation of scavengers, bawling mother cow). All necropsies were performed at the site of discovery, and bear depredation was assumed if tooth punctures or claw marks with subcutaneous hemorrhaging were present near the head or dorsal region (Roy and Dorrance 1976, Griffel and Basile 1981). We also measured deep muscle temperature when possible. If deep muscle temperature was above ambient temperature, we assumed death occurred the previous night (Smith et al. 1987*a*,*b*). When deep muscle temperature could not be obtained (e.g., carcass mostly consumed) or when body and ambient temperatures were not different, date of attack was estimated based on fly larva development and degree of decay.

Cattle owners gathered all remaining cattle following each grazing season and reported the number missing. We assumed missing cattle died on the study area. We estimated depredation of missing cattle by fitting mortality-sensing transmitters (Advanced Telemetry Systems, Incorporated, Isanti, Minnesota, USA) to 233 calves (32% of the calf population) before they arrived on BSA in 1995. Calves were separated from the cows, allowed to mix in large corrals, and the first 233 calves were radiotagged as they exited. We scanned for mortality signals daily and investigated all mortalities to determine cause of death. We tested the hypothesis that the proportion killed by bears was unrelated to whether the calf was marked using Fisher's exact test. We assumed bear depredation rates among necropsied calves represented those in missing calves if differences between marked and unmarked calves were not significant ($P \geq 0.05$).

We monitored bear-killed cattle carcasses for 1–2 nights after necropsy with night vision equipment, radio-telemetry, or both. Individual bears were considered responsible for kills if located at the site during the estimated time of attack or within 24 hours from nightly telemetry or carcass monitoring. Traps were set at the carcass if unmarked bears were suspected of being depredators. Bears captured at carcasses were radiotagged and released. We identified bears scavenging at carcasses by plotting bear locations and periodically inspecting carcasses for foraging activity or by monitoring carcasses at night with radiotelemetry.

After bear activity patterns were well established, we implemented various management actions to evaluate their utility in alleviating cattle losses. Habitual cattle depredators identified during the first 2 years of the study were targeted for subsequent management actions including (1) hazing the bear from the study area (i.e., aversive conditioning), (2) translocation >100 km, or (3) permanent removal (i.e., capture and euthanasia). Hazing consisted of displacing the target bear using loud noises (i.e., yelling, discharging firearms, vehicle horns) when it was actively pursuing cattle. In addition to management actions targeting specific individuals, cattle carcasses on BSA were removed or obliterated with explosives after necropsy during 1996 to reduce the carrion source. We examined potential decline in mean annual grizzly bear residency rates ($P < 0.05$) following carcass removal using a one-tailed *t*-test.

RESULTS

We captured 18 grizzly bears (12 male, 6 female; Table 1) during 3,465 trap nights, and documented the presence of 2 others (both females with dependent cubs). All captured bears except 1 yearling female were fitted with VHF (very high frequency) radiotransmitters. Shedding of transmitters and staggered capture dates limited monitoring to 6 (1994), 11 (1995), and 14 (1996) bears annually (Table 1). However, most were monitored for ≥2 field seasons ($n = 11$) or captured as dispersing subadults (3 year-olds) during 1996 ($n = 4$; Table 1). Seventeen black bears also were radiotagged and monitored during the study (Holm et al. 1999).

Cattle were located at least once in 33 of 35 survey blocks, and an east–west band of 14 blocks across the center of the study area contained cattle ≥ 20% of the combined grazing seasons. Cattle traveled in groups as they moved across the study area and were typically limited to 6.9 survey blocks/day (range = 2–13), resulting in localized densities of 22–77 cattle/km^2.

Bear Activity

Marked bears moved out of the study area in September after varied lengths of residency each spring and summer. Only 2 (bear 248 in 1995 and 274 in 1996) denned within the study area. Timing of fall movements was similar each year. Arrival dates, however, varied (median = 25 July, range = 17 June–9 August, $n = 10$). Fifteen of 17 bears spent <50% of their time in the study area while being monitored (Table 2). Subadult females had the highest mean residency rate (43.8%), followed by adult males (29.2%), adult females (21.4%), and subadult males (17.4%).

Fifteen of 17 bears monitored spent a greater proportion of time in the study area while depredations were occurring, and 10 of these were located near cattle more frequently than expected ($P < 0.05$, Table 2). Notably, 5

Table 1. Cohort, identification, age, and proportion of days monitored each grazing season for grizzly bears radiotagged in the Blackrock–Spread Creek and Elk Ranch East grazing allotments, northwest Wyoming, 1994–96.

			% days monitored[b]		
Cohort	ID	Age[a] (in 1994)	1994	1995	1996
Subadult male	225	1			75.0
	253	3		41.8	100.0
	274	1			100.0
	277	1			88.7
Subadult female	248	1		71.3	100.0
	279	1			70.2
	G52[c]	1			
Adult male	34	22	58.9		
	174	8		100.0	100.0
	203	14	78.3	100.0	100.0
	209	7	93.8	100.0	41.1
	224	6	10.0		65.3
	229	11	62.8	100.0	100.0
	251	6		50.8	100.0
	252	5		44.3	100.0
Adult female	166	10	94.6	100.0	
	179	6		77.0	100.0
	247	5		71.3	

[a] Age determined using cementum annuli techniques (Wyoming Game and Fish Laboratory, Laramie, Wyoming USA).

[b] Proportion of days bears were equipped and monitored with VHF radiotelemetry each grazing season. Monitoring periods began 10 Jun 1994, 17 Jun 1995, and 15 Jun 1996 and ended 16 Oct 1994–96.

[c] Bear was not radiomarked.

Table 2. Percent of transmitter-days[a] grizzly bears were located in the study area, significance of spatial association tests (Ludwig and Reynolds 1988) between bears and cattle for non depredation and depredation periods, and number of confirmed cattle depredations for grizzly bears radiomonitored on the Blackrock–Spread Creek and Elk Ranch East grazing allotments, northwest Wyoming, 1994–96.

		Non-depredation period[b]		Depredation period[c]		
Bear ID	% days in study area	% days in study area	Cattle association P-value	% days in study area	Cattle association P-value	No. of confirmed cattle depredations
34	78.9	58.3	>0.999	82.8	<0.001[d]	5
166	41.4	32.4	0.747	48.5	<0.001[d]	1
174	5.3	1.7	0.196	14.9	0.001[d]	0
179	12.4	5.3	0.036[d]	28.4	0.068	0
203	16.7	<1.0	>0.999	43.2[e]	<0.001[d]	16
209	35.7	13.4	0.001[d]	56.6	<0.001[d]	15
224	22.3	14.9	>0.999	32.2	0.024[d]	0
225	30.1	19.2	0.538	86.7	>0.999	0
229	19.9	6.5	0.075	45.5	<0.001[d]	1
247	10.3	8.1	>0.999	12.0	0.028[d]	0
248	74.9	73.6	0.652	77.6	0.054	0
251	36.6	35.7	0.014[d]	39.1	<0.001[d]	1
252	18.0	15.0	0.079	28.9	0.308	0
253	17.1	11.4	0.780	40.0	<0.001[d]	0
274	17.7	20.6	0.241	0.0	—	0
277	4.5	5.4	0.542	0.0	—	0
279	12.6	7.7	>0.999	55.6	>0.999	1

[a] Transmitter days = total grazing period x % days monitored.

[b] Non-depredation period: 10–15 Jun and 11 Sep–16 Oct 1994; 17 Jun–25 Jul and 14 Sep–16 Oct 1995; 15 Jun–13 Jul and 31 Jul–16 Oct 1996.

[c] Depredation period: 16 Jun–10 Sep 1994; 26 Jul–13 Sep 1995; 14–30 Jul, 1996.

[d] Significant results ($P < 0.05$) indicate positive spatial associations with cattle.

[e] Bear left the study area following aversive conditioning on 29 July 1996.

of 7 bears not spatially associated with cattle were subadults, 2 of which were completely absent from the study area while depredations were ongoing. Nine adults and 1 subadult had significant spatial associations with cattle during the depredation period; the single subadult (253) was the oldest subadult monitored. During the period when no depredations occurred, 3 bears were consistently located near cattle and 12 others spent <20% of their time in the study area (Table 2).

Cattle Losses and Depredation

Of the 262 cattle that died during the study, we located 193 and determined cause of death for 182 (Table 3). Success of finding dead cattle was similar among years and allotments, excluding ERA in 1994 when all missing cattle were discovered ($\bar{x}$ = 71%; χ^2 = 2.88, 4 df, P = 0.58). Bear depredation was evident in 39% (51 of 132) of calf and 12% (6 of 49) of adult mortalities we confirmed. Calves were the most common victims of bear- (90%) and non bear-caused deaths (65%), although proportions differed (χ^2 = 11.54, 1 df, $P < 0.01$). Of the 57 cases documented, bear depredation consistently occurred at night based on 9 times that we monitored bears during a depredation event (2230–0330 hrs) and 24 cases freshly killed carcasses discovered in the morning. Kills were separated by an average of 3 days (for those of known date, n = 50) and all were documented between 16 June–10 September 1994, 26 July–13 September 1995, and 14–30 July 1996 (median = 9 Aug; Fig. 2). We observed periods without bear depredation ($\bar{x}$ = 37 days, range = 6–78, n = 6) before and after each depredation period.

Sixty-nine missing cattle were never located and were assumed dead. Bears likely killed some of these because the composition of missing cattle (87% calves) more closely resembled cattle killed by bears (90%; χ^2 = 0.19, 1 df, P = 0.66) than those dying from other causes (65%; χ^2 = 10.54, 1 df, $P < 0.01$; Table 3). Moreover, we examined 10 marked and 22 unmarked dead calves on BSA during 1995. The proportion killed by bears did not differ between mark status (30% vs. 36%; χ^2 = 0.12, 1 df, P = 0.73), suggesting bear depredation rates among necropsied calves (51 of 132, 38.6%) may be representative of those in missing calves (n = 60) and calves dying of unknown causes (n = 11). Thus, we estimated an additional 27 (71 x 0.386) calf losses to bear depredation above those confirmed during necropsies (51 calves, 5 cows, and 1 bull; Table 3).

We identified the responsible bear in 40 of 47 confirmed attacks that were immediately fatal. All sex and age (subadult or adult) groups except subadult males killed cattle. Adult males, however, were the most frequent. Four bears, including 2 adult males (229 and 251), an adult female (166), and a subadult female (279) killed 1 calf each, whereas 3 adult males (203, 209, and 34) killed the remaining 36 (16, 15, and 5, respectively, Table 2). A decision between multiple suspects could not be made in 4 additional cases, but 3 were between 2 adult males and the fourth between 2 adult males and an adult female. In 3 of the 4 cases, the decision involved 1 or more of the adult males already identified as repeat offenders. Un-

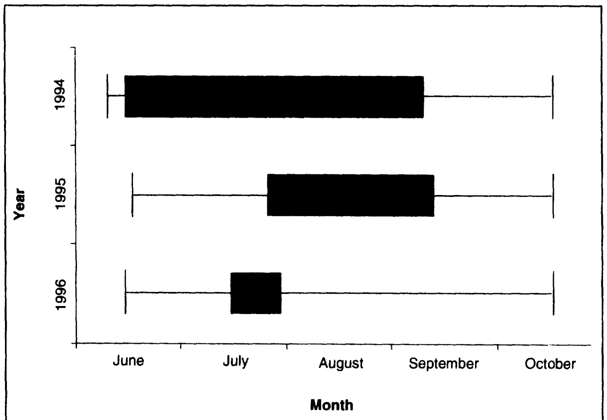

Fig. 2. Grizzly bear depredation periods (solid bars) during each grazing season (solid lines) on the Elk Ranch East and Blackrock–Spread Creek cattle allotments in northwest Wyoming, 1994–96.

Table 3. Number of cattle mortalities by cohort and cause (bear depredation, other, or unknown), and total estimated losses due to bear depredation on the Blackrock–Spread Creek and Elk Ranch East grazing allotments, northwest Wyoming, 1994–96.

	Cause of death				
Cohort	Bear n(%)	Other n(%)	Unknown n(%)	Missing n(%)	Total estimated bear depredation[a] n
Calf	51 (89.5)	81 (64.8)	11 (100.0)	60 (87.0)	78
Yearling	0 (0.0)	0 (0.0)	0 (0.0)	1 (1.4)	0
Cow	5 (8.8)	35 (28.0)	0 (0.0)	6 (8.7)	5
Bull	1 (1.8)	8 (6.4)	0 (0.0)	2 (2.9)	1
Total	57 (100.0)	125 (100.0)[b]	11 (100.0)	69 (100.0)	84

[a] Estimated bear depredation includes confirmed bear depredation from all cohorts (first column) and a proportion (38.6%) of missing calves and those dying from unknown causes, which was based on the observed depredation rate for calves during the study (51 of 132).

[b] Includes 1 animal of unknown cohort.

marked grizzly bears (1 or 2) were suspected in the remaining 3 cases. Black bears were not implicated in cattle depredation. In addition to the 47 immediately fatal bear attacks detected, 15 others included 10 cases where cattle escaped the initial attack but later succumbed to fatal injuries and 5 where cattle survived the attack. We were unable to identify the responsible bears in these 15 cases because time and location of the incident were unclear.

During 1985–91 mean annual calf loss rate was 2.5% on BSA. In contrast, it was 6.2% during our study. Calf mortality rate during our study was 5.1% after excluding necropsied calves killed by bears and 4.1% when a similar proportion of missing and unknown calf mortalities were omitted. Thus, calf losses not attributed to bears averaged 1.6% higher during our study than when bear depredation was unconfirmed (1985–91). Although not statistically significant ($t = -1.92$, 8 df, $P = 0.09$), this difference is arguably economically significant.

Management Actions

We targeted individuals identified as habitual depredators late in 1995 and during 1996. One of the 3 adult males identified as a habitual depredator (34) was killed north of the study area in September 1994 after acting aggressively toward a hunter. We translocated another bear (209) twice, once prior to the study in mid-July 1993 (103 km) and again in early September 1995 (114 km). In both cases he returned to the study area the following spring and resumed cattle depredation. We euthanized this bear in the study area on 4 August 1996 after he killed 11 cattle in 17 days. The third bear (203) left the study area within 2 weeks of arrival on 29 July 1996 following 2 nights of aversive conditioning. No depredations were detected after 30 July 1996 once all 3 habitual depredators were absent, unlike the previous 2 years when depredations continued into early September (Fig. 2).

We documented scavenging by 13 marked grizzly bears at 59 carcasses where cattle died from something other than bear depredation. Included in this group were all marked bears known to kill cattle except 1 subadult female (279). She was unmarked until 1996, however, when carcasses were being removed to prevent scavenging. Scavenging did not appear to lead to depredation because 7 of 14 scavengers were never documented killing cattle, and the 2 most active scavengers (166 was at 10 carcasses and 229 was at 14) were only known to kill 1 calf each. In 1996, all but 4 carcasses found with nearby bear activity ($n = 13$) were removed from BSA. Grizzly bear residency rates were lower than the previous 2-years when carcasses were not removed ($t = 2.11$, 25 df, $P = 0.02$). However, depredations continued despite use by fewer bears until adult males known to kill cattle were absent.

DISCUSSION

Cattle Depredation

Our findings suggest that grizzly bears from most sex–age cohorts will opportunistically prey on cattle. Older-aged males were the most common depredator, but even within this cohort individual propensities varied. Among the 8 adult males we monitored, 5 killed ≤1 cattle each, while the remaining 3 were implicated in 90% of all identifiable losses. Subadult males were the only group not associated with depredations, which may have been partially due to exclusion by adult males (Holm et al. 1999). Given the relatively high number of adult males we encountered (8 of 17), adult male exclusion may also contribute to infrequent depredation by other grizzly bear sex–age classes. Our observations are similar to findings reported in other studies. Horstman and Gunson (1982) found that most cattle depredation by black bears in Alberta was by mature males. Knight and Judd (1983) found that relatively few adult grizzlies of both sexes killed cattle during their study. Claar et al. (1986) reported that 18 grizzlies they monitored did not kill cattle, but the 2 that did were both male (1 adult, 1 subadult). However, neither grizzly study (Knight and Judd 1983, Claar et al. 1986) reported individual depredation rates, thus it is unknown whether those bears were habitual or infrequent depredators of cattle.

Black bears did not appear to depredate cattle during our study, which was surprising given the relatively high number of black bears we incidentally captured and were then monitored by Holm et al. (1999; 24 captured, 17 monitored). Although not frequently reported, several studies have documented black bear depredation on cattle (Davenport 1953, Roy and Dorrance 1976, Horstman and Gunson 1982, Bjorge 1983). Grizzly bears we monitored appeared to use different habitats than black bears, with differences most pronounced for areas occupied by adult male grizzlies (Holm et al. 1999). Thus, grizzlies may exclude black bears from cattle-occupied areas where these species occur sympatrically, thereby reducing the opportunity for black bears to prey on cattle.

Bear Activity Relative to Cattle on the Study Area

Our findings suggest a bear's presence near cattle does not indicate depredatory behavior, contrary to what has been suggested historically (e.g., Murie 1948). Most bears we monitored exhibited a significant spatial association with cattle while depredations were occurring, but few preyed on cattle. Some bears were depredators, some were scavengers, and yet others coincidentally shared cattle range (e.g., during the non-depredation period).

Our anecdotal observations suggested that depredatory behavior by bears produced noticeable changes in cattle behavior, while non-depredatory bears traveling near cattle did not. Cattle became clumped when depredation was occurring, leading to localized depletion of forage, and range managers were frequently forced to drive cattle back onto desirable grazing areas. Conversely, cattle were more scattered and sedentary when depredation was absent. On several occasions we observed bears traveling near cattle that were alert but otherwise calm. In all of these cases, the bear was not displaying depredatory behavior, and 1 of these observations included a known cattle killer.

Range managers on BSA contended that depredatory bears caused increased stress to livestock, which exasperated illness symptoms thereby reducing survival rates. Mortality from larkspur (*Delphinium* spp.) poisoning and pneumonia may increase among excited cattle, but the outcome of fatal illnesses, such as brisket disease, would not be affected (Fraser 1991). We did not determine causes of non bear-caused cattle mortalities, but both larkspur poisoning and brisket disease were commonly suspected. If the estimated number of calf losses resulting from bear depredation is excluded, an increase of 1.6% in the mean annual loss rate was observed during the study compared to losses observed prior to documented bear depredation (before 1992). Whether this increase is due to underestimating calf losses, stress from predatory bears chasing cattle, or other biological and environmental factors besides grizzly bear activity is unknown. We are unaware of factors that may have led to underestimating bear-caused calf losses because our use of mortality transmitters appeared to provide an unbiased sample in 1995. Furthermore, we maximized discovery of dead calves by investigating all possible indicators such as a bawling mother cow or sightings of scavengers.

Removal of Cattle Carcasses

Bears were noticeably less concentrated in the study area during the1996 grazing season. A number of interrelated factors could have been responsible including: (1) a reduction of carrion from fewer cattle losses following removal of depredating bears, (2) carcass removals, which occurred only in 1996, (3) bears stopping (e.g., 174, 179, 252) or reducing (203, 225, 253) use of the study area during 1996, although others appeared unaffected (229, 248, 251; Table 2), and (4) bears seeking other areas with good food conditions. Whitebark pine production was high in 1996 throughout the Yellowstone Ecosystem (Knight and Blanchard 1997), and use of moth aggregation sites increased following several years of low use (Ternent and Haroldson 1999). Yet, relatively good food conditions were also observed during 1995 when bears were extremely concentrated near cattle.

Redistribution of livestock carrion has reduced human–grizzly bear conflicts (Madel 1996) and could be useful in reducing cattle losses. Success of redistributing or removing cattle carcasses appears limited, however, because depredatory bears continued to prey on cattle despite the reduction of carrion during our study. Similar to Claar et al. (1986) and Madel (1996), we found no evidence that bears scavenging cattle carcasses became cattle killers during our 3-year study. BSA loss records since 1985 suggest low calf mortality until 1993 ($\bar{x} = 2.5\%$ or 13 calves annually), and at least 1 depredating bear we identified (34) appeared to use the study area during that period based on historic capture records (Trophy Game Section, Wyoming Game and Fish Department, Lander, Wyoming, USA). Thus, while carcass removal may reduce the concentration of bears in an area, it may not prevent bears from developing depredatory tendencies or repel depredating bears from grazing areas.

Management Actions Targeting Depredatory Grizzly Bears

We successfully hazed 1 depredating bear from cattle during the 1996 grazing season that, together with removal of another depredating bear, terminated bear depredation during the remainder of the grazing season. However, weak transmitter strength and low search intensity outside the study area prevented us from determining if the hazed bear moved to another cattle allotment. We attempted hazing the same bear from BSA again during the 1997 grazing season (following this study) without success. Thus, hazing bears from cattle may only provide temporary and local relief, analogous to translocating bears. This approach, however, may be useful in sensitive situations where the target individual is considered important in maintaining population viability (e.g., adult females).

Adult grizzly bears that are translocated typically return to their original home range, but relocations of subadults can sometimes be permanent (Blanchard and Knight 1995). In our study, the time required for adult male bear 209 to return extended into the next grazing season after 2 separate translocations. Thus, distant translocations could provide relief for the immediate grazing season or longer in some circumstances. Additionally, this practice combined with radiomarking allows discrimination between habitual and opportunistic depredators, which appears to be a key component of grizzly bear management on rangelands. During our study, cattle depredation was limited to a discrete period rather than occurring continually throughout the grazing season. If problem bears had been captured and moved at the onset of depredations, losses likely would have been reduced. In cases involving habitual depredators, however, the reappearance of problem individuals is expected and translocation efforts are not a long-term solution.

Bears may also become increasingly difficult or virtually impossible to capture after repeated translocations (this study), increasing time and effort recapturing them. Difficulties associated with recapturing problem bears tend to foster non-selective removal methods (i.e., remove any bear captured after 5 depredation events; U.S. Fish and Wildlife Service 1999). New techniques that remotely mark animals (e.g., auto-attach telemetry collars; Shivik and Martin 2000), thereby avoiding large time commitments of capturing trap-shy animals, should enhance the success of future grizzly bear management.

Unfortunately, we were unable to identify management techniques that were as effective as permanent removal in alleviating cattle losses. Based on conversations with local ranchers, nondiscriminatory removal resulted in the substantial reduction of grizzly bears from Wyoming rangelands shortly after Murie's (1948) study. Our findings suggest that relatively few removals are necessary if highly selective techniques are applied. Habitual depredators in our study tended to be older-aged males. Removal of these individuals should have minimal impact on the long-term survival of the population, because demographic characteristics of this cohort are less influential than adult females (Knight and Eberhardt 1985). Thus, if repeated depredations are limited to a few individuals and other management techniques ultimately fail (e.g., translocation, hazing), removal may be a reasonable management option for resolving cattle–bear conflicts.

We did not identify the factors leading to the development of depredatory behavior, which merits further investigation. Scavenging did not appear to encourage depredatory behavior, and depredatory tendencies varied among and within cohorts. One drawback to permanent removal is that immigrants might move into the area and become chronic depredators, thereby creating a population sink (Knight et al. 1988). Similarly, if habitual depredators are females and their future reproductive potential is considered crucial to the population, management actions may be limited to non-lethal techniques. Nevertheless, in areas of high human activity, removal of chronic nuisance bears should benefit the bear population by increasing public tolerance for grizzly bears and their expansion.

Comparisons between Grizzly Bear–Cattle Interactions on BSA from 1945–46 and 1994–96

In reviewing Murie's (1948) study on BSA 49 years earlier, we noted a few similarities. First, depredatory bears selected juvenile over adult cattle. Seventy-five-percent of depredated cattle included calves and the remaining 25% were yearlings (Murie 1948). Yearling cattle were much more common on BSA in the 1940s than during our study, but bear depredation of calves was commonly observed in both studies. Second, Murie's results implied that adult male bears might have been the primary culprits, similar to our observations. While Murie was unable to identify individual bears (largely due to technological limitations), he reported track sizes ($n = 4$) that were similar to adult males we monitored (15–17 cm wide) and in 2 cases he captured males (possibly adults) at depredated carcasses. Third, both studies failed to detect black bears as cattle depredators despite their presence.

Some differences between the 2 studies also were apparent. Although time of depredation could not be determined in most cases, Murie (1948) suggested daytime depredation in 4 incidents where fresh carcasses were discovered. Our findings suggest grizzlies killed cattle at night. One possible explanation is that bears experienced more disturbances from human activity during our study than 5 decades ago. Vehicle access and recreational use have noticeably increased in BSA since then. Another difference was that Murie noted bear depredation during July and early August, whereas we documented depredation into early September. He also reported that losses were minimal on ERA (then referred to as the Moran Allotment), but we observed significant losses on both ERA and BSA. Grazing practices were similar during both studies, but differences in distribution and length of cattle depredations may have been due to differences in the number of depredators present. The 3 depredatory bears we identified selected cattle from different segments of the study area corresponding to each of their home ranges (Anderson et al. 1997). Although Murie suspected most resident grizzlies were cattle killers, the limited timing and location of cattle losses suggests that actually few depredators may have been involved. Murie suspected multiple bears because intensive control (7–9 grizzly bears were killed in or near the study area during 1945) failed to reduce problems. Control methods described by Murie, however, were nonselective. Thus, it is possible the offending individual(s) was not removed, leading to the perception of widespread depredatory behavior.

MANAGEMENT IMPLICATIONS

Given the delicate nature of the Yellowstone grizzly bear population, both politically and biologically, future management actions should be applied cautiously. Although the success of translocating bears has been scrutinized because many return to their capture site (Blanchard and Knight 1995) or become conditioned to avoid recapture (our observations), it does allow discrimination between habitual and opportunistic depredators and provides temporary relief. New techniques allowing more efficient identification of habitual depredators should continue to be investigated (e.g., remotely attached telemetry collars; Shivik and Martin 2000). In addition, there may be some merit to applying aversive conditioning techniques (e.g., hazing) on rangelands. However, hazing results are dependent on a bear's sensitivity to disturbance, and though a bear may leave a problem area, the action should not be considered successful if the bear continues depredatory behavior elsewhere. In chronic depredation situations, permanent removal of depredating bears or cattle may be the only long-term solution. Cattle owners should not be expected to endure excessive losses or abandon all areas inhabited by grizzly bears. This only heightens animosity toward bears and erodes support for population recovery.

Our findings suggest that a relatively small segment of the grizzly bear population is associated with the majority of cattle losses. As a result, several management alternatives including removal, translocation, and aversive conditioning are available depending on the severity and circumstances of the situation. The Yellowstone grizzly bear population appears to be expanding into currently unoccupied areas (Gunther et al. 1999). If range expansion is to continue to enhance the long-term survival of the population, management programs should be designed to increase tolerance of grizzly bears by balancing the conservation of individuals with attempts to alleviate human–bear conflicts. Over 50 years ago Murie (1948) concluded: "Because the grizzly range in the United States is now so greatly restricted it is believed by many that the grizzly should be given special consideration in this region. A satisfactory solution will require land-use planning on a high plane, with all social needs carefully considered." It seems little has changed. Grizzlies were apparently extirpated or greatly reduced from Wyoming rangelands shortly following Murie's study, but have recently returned.

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