Rates and Causes of Grizzly Bear Mortality in the Interior Mountains of British Columbia, Alberta, Montana, Washington, and Idaho

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RATES AND CAUSES OF GRIZZLY BEAR MORTALITY IN THE INTERIOR MOUNTAINS OF BRITISH COLUMBIA, ALBERTA, MONTANA, WASHINGTON, AND IDAHO

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Abstract: Trends of grizzly bear (*Ursus arctos*) populations are most sensitive to female survival; thus, understanding rates and causes of grizzly bear mortality is critical for their conservation. Survival rates were estimated and causes of mortalities investigated for 388 grizzly bears radiocollared for research purposes in 13 study areas in the Rocky and Columbia mountains of Alberta, British Columbia, Montana, Idaho, and Washington between 1975 and 1997. People killed 77–85% of the 99 grizzly bears known or suspected to have died while they were radiocollared. In jurisdictions that permitted grizzly bear hunting, legal harvest accounted for 39–44% of the mortalities. Other major causes of mortality included control killing for being close to human habitation or property, self-defense, and malicious killings. The mortality rate due to hunting was higher (P = 0.006) for males than females, and subadult males had a higher probability (P = 0.007) of being killed as problem animals than did adult males or females. Adult females had a higher (P = 0.009) mortality rate from natural causes than males. Annual survival rates of subadult males (0.74–0.81) were less than other sex–age classes. Adult male survival rates varied between 0.84 and 0.89 in most areas. Survival of females appeared highest (0.95–0.96) in 2 areas dominated by multiple-use land and were lower (0.91) in an area dominated by parks, although few bears were killed within park boundaries. Without radiotelemetry, management agencies would have been unaware of about half (46–51%) of the deaths of radiocollared grizzly bears. The importance of well-managed multiple-use land to grizzly bear conservation should be recognized, and land-use plans for these areas should ensure no human settlement and low levels of recreational activity.

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Due to late maturation and a low reproductive rate, the trend of a grizzly bear population is most sensitive to a change in female survival (Knight and Eberhardt 1985, McLellan 1989, Eberhardt et al. 1994, Hovey and McLellan 1996, Mace and Waller 1998). Grizzlies, however, are vulnerable to several forms of human-caused mortality. They are prized trophies for hunters and a valuable source of Asian medicine (Mills and Servheen 1994). During some encounters with people, grizzlies are viewed as a threat and shot in self-defense. These bears are also attracted to human habitation where they are often destroyed or captured and moved.

Minimizing grizzly bear mortality, particularly of adult females, is the key to grizzly bear conservation in small, threatened populations (U.S. Fish and Wildlife Service 1993, Mattson et al. 1996). Limiting mortality to a sustainable level is the primary management objective in other areas (Alberta Fish and Wildlife Division 1990, Province of British Columbia 1995). Managers usually set a maximum acceptable human-caused mortality rate of 2–6% of the estimated population (Alberta Fish and Wildlife Division 1990, Miller 1990, Province of British Columbia 1995) but must guess at the number and causes of undetected deaths. Knowing the actual causes and rates of grizzly bear mortality is critical to grizzly bear conservation.

Because grizzly bears are difficult to capture, frequently lose radiocollars, and usually have low mortality rates, individual research projects rarely collect sufficient information on mortality factors to make general inferences. In addition, factors influencing mortality rates and causes

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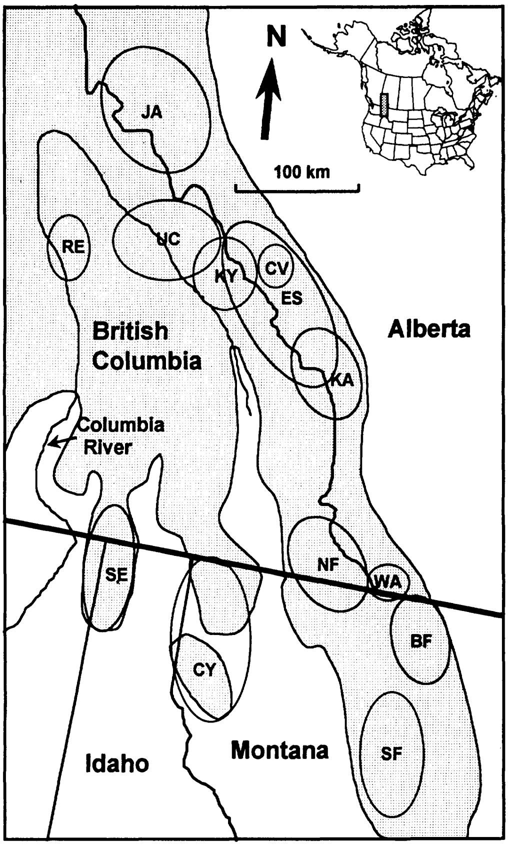

Fig. 1. Location of 13 study areas providing data on mortality rates and causes for grizzly bears in the Rocky and Columbia mountains, 1975–97; where JA is Jasper National Park, RE is Revelstoke, UC is Upper Columbia, KY is Kootenay–Yoho National Parks, CV is Cascade Valley, ES is Eastern Slopes, KA is Kananaskis, SE is Selkirk Mountains, CY is Cabinet–Yaak Mountains, NF is North Fork of the Flathead River, WA is Waterton National Park, BF is Blackfeet Indian Reservation, SF is South Fork of the Flathead River. The shading represents the approximate distribution of grizzly bears in the area.

may vary among areas, making extrapolations potentially misleading. We used data from several telemetry-based studies in areas with a variety of management goals to estimate and compare grizzly bear mortality rates and causes. We also estimated the proportion and types of grizzly bear deaths that would not have been recorded by management agencies unless the grizzly bears had been radiocollared.

STUDY AREA

We used data from 13 study areas in the Rocky and Columbia mountains of British Columbia, Alberta, Montana, Idaho, and Washington collected between 1975 and 1997 (Fig. 1). Topography of all study areas was mountainous, but climate and resulting ecosystems varied from relatively mild and wet habitats near Revelstoke, British Columbia (Achuff et al. 1984) to dry, cold ecosystems in Jasper National Park (Holland 1976). Although grizzly bear diets varied among areas, they generally relied on roots and tubers, graminoids (Cyperaceae, Gramineae), horsetails (*Equisetum* spp.), and members of the carrot family (Umbelifferae) in the spring. During summer and fall, huckleberries (*Vaccinium* spp.) and buffalo berries (*Shepherdia canadensis*) dominated their diet. Grizzly bears in all study areas consumed ungulates when encountered, but none had access to anadromous salmon (*Oncorhynchus* spp.; Mace and Jonkel 1986, Hamer and Herrero 1987, McLellan and Hovey 1994).

Study areas contained varying amounts of protected areas and a diversity of human activities. Studies in Cascade Valley, Alberta, (Hamer and Herrero 1987) and Waterton, Alberta, each focused on 2 female grizzly bears that remained almost exclusively in national parks. The Eastern Slopes, Yoho–Kootenay, and Jasper studies were based in national parks but also included lands outside park boundaries. The Upper Columbia and Kananaskis (Carr 1989, Wielgus and Bunnell 1994) study areas were almost equally in and out of parks. The Eastern Slopes and Upper Columbia study areas contained rural and urban settlements both in and outside park boundaries.

The remaining 6 study areas were primarily outside protected areas, but radiocollared grizzly bears used adjacent parks and designated wilderness. Intensity of human uses varied among these 6 areas. In the South Fork of the Flathead River (SF Flathead) study area, multiple-use lands with extensive forest management and outdoor recreation met an abrupt transition with rural and urban areas (Mace and Waller 1997*a*). Rural settlement, ranching, and some oil and gas development occurred within the Blackfeet study area. There was limited human settlement in and adjacent to the Cabinet–Yaak, North Fork of the Flathead (NF Flathead), and Selkirk study areas. Timber harvest was common in these areas, as was gas exploration in the NF Flathead. There was only 1 residence in the Revelstoke study area, but timber harvest was common.

Grizzly bear hunting was regulated by a quota for guides and their nonresident clients and a limited entry draw or lottery for resident hunters in Alberta and British Columbia. A strict quota system was permitted in Montana, excluding the Cabinet–Yaak areas, until 1991, when hunting was closed. Grizzly bear hunting was not permitted in Idaho or Washington. The NF Flathead and Revelstoke studies were the only areas that had grizzly bear hunting over most of the study area and over the duration of study. Hunting for other species was permitted in all study areas, excluding portions in national and some provincial parks.

METHODS

Grizzly bears were captured for research purposes with foot snares or in culvert traps set throughout the study areas, and immobilized to allow handling. Some grizzly bears were darted from a helicopter. No grizzly bears were first captured as problem animals. A premolar was removed from subadults and adults for aging (Stoneberg and Jonkel 1966), and grizzly bears were classified as cubs (<1 yr old), yearlings (1 yr old), subadults (2–5 yr old), and adults (≥6 yr old). Except for bears captured and radiocollared before 1980, radiocollars were attached with a canvas connector that decomposed and allowed the radiocollar to drop from the grizzly bear after a planned amount of time (1–5 yr). Not only did these canvas connectors result in fewer neck injuries, but radiocollars were usually shed when transmitting; hence, fates of grizzly bears at the end of the monitoring period were clear. Most radiocollars were sensitive to movement and changed pulse rate after 4–6 hr of inactivity, after the radiocollar was shed, or the grizzly bear had died.

Cause of death of radiocollared grizzly bears was determined by a variety of methods. The Cascade Valley and Waterton studies relied on ground tracking, but none of the grizzly bears in those studies died while being monitored. In the other studies, radiocollared grizzly bears were located from fixed-wing aircraft 2–8 times/month in addition to supplemental ground tracking. If a change in radio pulse rate was detected, the site was investigated, usually within 1 week, and the dropped radiocollar retrieved or the cause of mortality determined. Because radiocollars on hibernating grizzly bears often switch pulse rates, 2 grizzly bears that died during or near to the denning period were investigated several months after they had died. Grizzly bears killed as problem wildlife, for defense of life or property, taken legally by hunters, and some illegal killing were reported to or investigated by conservation officers.

Mortalities were first classified as natural, human-caused, or unknown. Deaths were classified as natural when a natural cause was evident. In 3 cases, deaths were classified as natural without clear evidence of a natural cause, but the carcasses were found in locations rarely if ever visited by people. In some cases, it was not possible to determine whether a death was natural or human-caused. These mortalities were classified as unknown.

Mortalities classified as human-caused were further categorized by the apparent reason: (1) legal hunting; (2) malicious, where the animal was shot and left for no apparent reason; (3) management problem, when the bear was near buildings, camps, or livestock, and killed or removed by a wildlife official; (4) citizen's problem, when a citizen shot the bear for being near buildings, livestock, or a camp; (5) self-defense, when a person thought their safety was threatened; (6) poached, when the animal was hunted but killed illegally; (7) accident, such as a vehicle collision; (8) unknown, when a radiocollar had been cut off; and (9) research, when death was capture-related. Deaths due to research were excluded from analyses. The legality of killings was not specifically addressed, because of different laws among jurisdictions and inconsistencies in legal systems.

Suspected human-caused deaths were recorded when the radio signal from a grizzly bear that had been located near human residences or camps disappeared prematurely. For example, when 2 radiocollared subadults that traveled together disappeared concurrently after being located in an area with many homes, their deaths were suspected. In another case, not only was the radiocollared grizzly bear located near a hunting camp before the radiocollar disappeared, but a blood trail was found at the camp.

For each confirmed or suspected grizzly bear mortality, we determined whether or not the management agency would have recorded the death if the animal had not been radiocollared. Unrecorded cases were those only reported by researchers after the radiocollar changed pulse rate and the site was investigated. There was a chance that some of these dead grizzly bears may have been found and reported. However, after cause of death was ascertained, carcasses were usually left in the field, and in no cases were they later reported. Similarly, grizzly bears were not discovered if they were killed and had their radiocollars cut off and discarded.

Although we assumed grizzly bears monitored during each study were representative samples for that time and place, we were forced to pool data because of small sample sizes. Data were pooled by study areas into groups with similar management goals and geographic proximity. The Jasper, Cascade Valley, Eastern Slope, Upper Columbia, Yoho–Kootenay, and Kananaskis studies were based in the contiguous Canadian national and provincial park complex. Some radiocollared bears moved between 2 or more of these study areas, so data were pooled into the study area group called Mountain Parks. Because Waterton and the Blackfeet Indian Reservation are adjacent and some bears moved between study areas, they were pooled and called the Blackfeet–Waterton. Although the Cabinet–Yaak is geographically separated from the Selkirks, we pooled data from these studies because management objectives were similar. The NF Flathead and SF Flathead study areas were geographically isolated and had large enough sample sizes to remain separate. Data from Revelstoke grizzly bears were not used in survival rate calculations, because sample sizes were small and geographic isolation prevented pooling with other studies. Revelstoke data were used in cause of death analyses.

Survival rates were estimated for each sex–age class (ad M, ad F, subad M, subad F) from each study area group via censored data from grizzly bears that were tracked for a minimum of 20 days. We used the following Kaplan-Meier estimator described by Hovey and McLellan (1996) to determine annual survival rates ($\hat{S}_i$):

$$\hat{S}_i = \prod_{j=1}^{n=52} \left[1 - \left(\frac{D_{ij}}{R_{ij}}\right)\right], \qquad (1)$$

where D_{ij} was the number of recorded deaths, and R_{ij} was the number of animals at risk for age class i during week of the year j (j = 1 [Jan 1–7], j = 2 [Jan 8–15], . . ., j = 52 [Dec 24–31]).

We applied Equation 1 to our data by using the following procedure. For each grizzly bear, the dates radiotracked were partitioned into week of the year. The sample at risk (R_{ij}) was increased by 1 for every week that a grizzly bear was radiotracked. Grizzly bears that were radiotracked >1 year had 1 record added to R_{ij} for every year they were monitored during week j. If the grizzly bear died, then D_{ij} was also increased by 1. Grizzly bears that lost radiocollars during week j were treated as censored and R_{ij} was reduced. If these individuals were recaptured, they were added to the sample at risk as a new record. Because grizzly bears were not radiocollared simultaneously, we treated the radiotracked sample as a staggered-entry design (Pollock et al. 1989). We used 5,000 bootstrapped samples (Efron and Gong 1983) to estimate bias and standard errors.

We tested differences in survival rates among study area groups and sex–age classes via an unbalanced, 2-way analysis of variance (ANOVA; Montgomery 1991). We performed a prospective power analysis of this ANOVA to determine appropriate sample sizes for future research based on our results (Cohen 1977). For the power analysis, both minimum and maximum power curves were derived via the mean square error of the ANOVA, with the experimentwise error rate and detectable difference set to 0.05. Differences in mortality rates associated with different causes were analyzed as a 1-way ANOVA with sex–age class as the design factor. We used the method of least-significant difference (Milliken and Johnson 1992) to test for pairwise differences between levels of significant factors. For these tests, we used Bonferroni's correction to determine the significance level. The power analysis and calculation of F-ratios, t-statistics, and P-values were performed with SAS programs (SAS Institute 1988) we developed for these analyses.

Because each jurisdiction had different management goals, practices, and laws, it is most valuable to discuss results by jurisdiction. For this reason, we summarized causes of mortality by jurisdiction. Unfortunately, survival rates could not be estimated for each jurisdiction, because radiocollared grizzly bears frequently moved among them. Instead, we calculated survival rates by sex–age class for each study area group.

RESULTS

A total of 388 grizzly bears was radiocollared and monitored for a total of 704.4 radiotracking years in the 13 telemetry studies. Of these grizzly bears, 90 (23%) were known to have died and 9 (2.3%) were suspected to have died while radiocollared. Seven of the 90 known deaths

Table 1. Estimated annual survival rates of adult and subadult (excludes radiocollared cubs and yearlings and Revelstoke data) grizzly bears of each sex by groups of study areas in the Rocky and Columbia mountains, 1975–97.

Age–sex Study area	No. bears	Mortalities (suspected)	Radio-years	Survival rate	SE
Adult female					
Mountain Parks	41	6	65.5	0.905	0.036
NF Flathead	31	4	89.9	0.959	0.021
SF Flathead	14	6	50.0	0.888	0.043
Selkirk–Yaak	18	3	57.9	0.952	0.026
Blackfeet–Waterton	14	0(2)	22.4	0.918	0.055
Combined	118	19(2)	285.7	0.926	0.006
Adult male					
Mountain Parks	50	7	55.8	0.891	0.038
NF Flathead	24	4	35.1	0.887	0.054
SF Flathead	12	3	25.4	0.888	0.062
Selkirk–Yaak	18	5	27.8	0.842	0.066
Blackfeet–Waterton	7	3	7.0	0.625	0.180
Combined	111	22	151.1	0.877	0.006
Subadult female					
Mountain parks	14	1	17.8	0.954	0.045
NF Flathead	25	3	46.5	0.935	0.036
SF Flathead	18	5	35.2	0.872	0.054
Selkirk–Yaak	10	1	9.5	0.929	0.070
Blackfeet–Waterton	13	3	19.5	0.859	0.077
Combined	80	13	128.5	0.923	0.008
Subadult male					
Mountain parks	29	8	24.6	0.742	0.078
NF Flathead	36	5(4)	36.4	0.782	0.063
SF Flathead	11	4	15.4	0.784	0.095
Selkirk–Yaak	16	4	18.7	0.807	0.090
Blackfeet–Waterton	17	3	12.1	0.798	0.106
Combined	109	24(4)	107.2	0.801	0.007

were due to research. Survival rates differed among sex–age classes ($F_{3,351}$ = 3.89, P = 0.009), but not among study area groups ($F_{3,351}$ = 0.69, P = 0.559). The interaction between sex–age and study area groups was not significant ($F_{9,351}$ = 0.52, P = 0.861). The annual survival rates of adult males, adult females, and subadult females were not different, but all were greater than the survival of subadult males (Table 1). Given the variability in survival rates and time that grizzly bears carried functioning radiocollars, our results indicated that about 42 grizzly bears should be radiocollared in each of the 16 sex–age study group categories to be 80% sure of detecting a survival rate difference of 0.05 (Fig. 2).

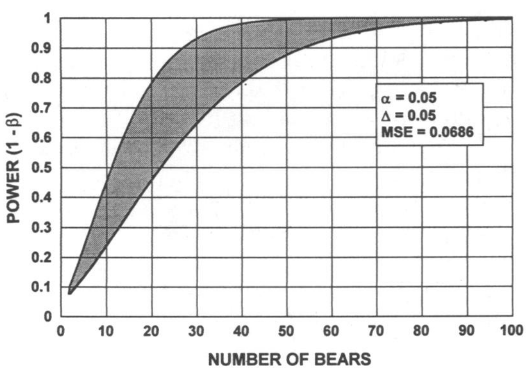

Fig. 2. Maximum (upper curve) and minimum (lower curve) statistical power as a function of sample size in each sex–age by study area group category for a 2-way analysis of variance F-test. The power curves were determined with α = 0.05 (experimentwise error rate) and Δ = 0.05 (detectable difference).

Depending on how the 9 suspected deaths and 5 deaths from unknown causes were treated, people caused 77–85% of the grizzly bear deaths (Table 2). Reasons that people killed grizzly bears varied among jurisdictions. Grizzly bear hunting was legal in British Columbia and Alberta, but it was only a major cause of mortality of radiocollared bears in British Columbia, where it accounted for 39–44% of the deaths. Ungulate hunters killing grizzly bears in self-defense, hunters mistaking a grizzly bear for a black bear (*Ursus americanus*), and malicious killing were major causes of grizzly bear deaths in Montana. Being shot or translocated by wildlife officials or shot by a citizen for killing live-

Table 2. Number of known mortalities of radiocollared grizzly bears in the Rocky and Columbia mountains, 1975–97, that would have been recorded by the management agency in each jurisdiction, including the number of additional known ( ) and suspected mortalities [ ] that would not have been detected without the aid of radiotelemetry.

Cause of death	Jurisdiction							
	Alberta	British Columbia	Idaho	First Nation	Montana	Washington	National park	Total
Natural	0	(8)	0	0	(4)	0	(2)	(14)
Unknown	0	(2)	0	0	(3)	0	0	(5)
Human-caused								
Hunter kill	1	15	0	0	0	0	0	16
Citizen problem	0(1)	0(1)[1]	0	1(1)	1	0	0	2(3)[1]
Management problem	1	1	0	2	5	0	1	10
Misidentification	0	0	0(1)	0	2(2)	0	0	2(3)
Self defense	1	1	0	0	3(1)	0	0	5(1)
Accident	0(1)	0	0	0	0	0	1	1(1)
Poach	0(1)	2(1)	1	0	0	2	0	5(2)
Malicious	0	1	0	0(2)	0(4)	0	0	1(6)
Unknown	0	(2)[3]	(1)[1]	(1)[2]	(2)[2]	0	0	0(6)[8]
Total: human-caused	3(3)	20(4)[4]	1(2)[1]	3(4)[2]	11(9)[2]	2	2	42(22)[9]
Total: all deaths	3(3)	20(14)[4]	1(2)[1]	3(4)[2]	11(16)[2]	2	2(2)	42(41)[9]

stock or being near homes or camps was a major mortality factor in several jurisdictions. Poachers rarely killed radiocollared grizzly bears, and there was no evidence of a radiocollared grizzly bear dying after being wounded by a hunter (wounding loss). People killed grizzly bears for unknown reasons in most studies.

Without the aid of radiotelemetry, management agencies would have been aware of only 46–51% of radiocollared grizzly bear deaths and 54% (if the 5 unknowns and 9 suspected were killed by people) to 66% of human-caused deaths. A large proportion of radiocollared grizzly bears in British Columbia was killed legally and reported by hunters, but even in British Columbia the management agency would have recorded only 53–59% of the mortalities and 67–83% of the human-caused deaths. In Montana, where there was little legal hunting of grizzly bears while radiocollared grizzly bears were being monitored, and no radiocollared grizzly bears were shot by hunters, agencies would have recorded 38–41% of the deaths and 44–55% of the human-caused deaths.

Mortality rates due to hunting differed among sex–age classes ($F_{3,425}$ = 4.17, P = 0.006), with adult and subadult males having similar rates that were higher than adult or subadult females. Mortality rates due to a combination of management and citizen control killing also differed among sex–age classes ($F_{3,425}$ = 4.06, P = 0.007), with subadult males having a higher rate than the other 3 age classes. Mortality rates from a combination of the clearly illegal categories of poaching, malicious killing, and killing for unknown reasons (radiocollars cut off) did not differ among sex–age classes ($F_{3,425}$ = 1.89, P = 0.131). Mortality rates from other human causes (accidents, misidentification, self defense) differed among sex–age classes ($F_{3,425}$ = 2.80, P = 0.040). Adult males had a higher rate than adult females, as 5 adult males but no adult females were shot in self-defense (Table 3). Natural mortality rates differed among sex–age classes ($F_{3,425}$ = 3.83, P = 0.010), with adult females having a higher rate than adult or subadult males. Twelve females died of natural causes: 3 in rock or snow avalanches, 1 in a collapsed den, 5 apparently by conspecifics, and 3 by unknown causes (Table 3).

DISCUSSION

Grizzly bears, particularly those without access to anadromous salmon, occur at low den-

Table 3. Age–sex class of known mortalities of radiocollared grizzly bears that would have been recorded by the management agency, including the number of additional known ( ) and suspected mortalities [ ] that would not have been detected without the aid of radiotelemetry.

Cause of death	Age–sex class				Total
	Adult female	Adult male	Subadult female	Subadult male	
Natural	(10)	0	(2)	(2)	(14)
Unknown	(2)	0	0	(3)	(5)
Human-caused					
Hunter kill	2	10	0	4	16
Citizen problem	0	(1)	1	1(2)[1]	2(3)[1]
Management problem	1	3	1	5	10
Misidentification	1	0	1(3)	0	2(3)
Self defense	0	4(1)	0	1	5(1)
Accident	0	(1)	1	0	1(1)
Poach	1	1(1)	1	2(1)	5(2)
Malicious	1(1)	(1)	(2)	(2)	1(6)
Unknown	(1)[3]	(1)	(2)[1]	(2)[4]	(6)[8]
Total: human-caused	6(2)[3]	18(6)	5(7)[1]	13(7)[5]	42(22)[9]
Total: all deaths	6(14)[3]	18(6)	5(9)[1]	13(12)[5]	42(41)[9]

sities (McLellan 1994, Miller et al. 1997) but require adult female survival rates of about 0.90 or greater to persist and be available for study (Eberhardt 1990, Mace and Waller 1998). Due to low densities and high survival rates, it is difficult to collect sufficient survival data for comparisons in an ecologically meaningful spatial and temporal scale. For example, after 10 years of research in the SF Flathead, Mace and Waller (1998) determined that the grizzly bear population had most likely been decreasing (λ = 0.977, 95% CI = 0.875–1.046). In contrast, after 15 years of research in the NF Flathead, Hovey and McLellan (1996) found the population had been rapidly increasing (λ = 1.085, 95% CI= 1.032–1.136). Even for these 2 populations with very different trends, we still could not detect a significant difference in adult female survival rates, particularly when 2 other study area groups were added to an ANOVA.

The power analysis further demonstrates this problem. A 5% difference in survival rate is biologically significant for grizzly bears (Eberhardt 1990), but we should have monitored many more grizzly bears of each sex–age class in each of the study area groups to detect this difference. Due to the difficulty of detecting statistical significance for the biologically significant phenomenon of a small difference in grizzly bear survival rates, we believe it is valuable to identify important trends even if statistical confidence may be lacking.

Subadult male grizzly bears had lower survival rates than other sex–age classes, and this rate was consistent among study areas. Perhaps due to their large ranges (Blanchard and Knight 1991, Mace and Waller 1997*b*) and inexperience, young males are more prone to encounter human attractants and be killed as problem bears than other sex–age classes. Where hunting was permitted, both subadult and adult males were more likely to be legally harvested than females. Different vulnerability to hunting was likely due to females with cubs or yearlings being legally protected, males having larger ranges, and some hunters selecting large-bodied males.

Although grizzly bear hunting selects males over females and was permitted in some study area groups but not others, adult males had similar mortality rates in all areas except the Blackfeet–Waterton, where sample sizes were very small. Survival rates of adult males in our study areas were similar to the 0.84 recorded in a hunted population on Chichagof Island (Titus and Beier 1994), but higher than the 0.75–0.80 recorded in the Susitna Drainage of Alaska. The Susitna population was being intentionally reduced in an attempt to increase survival of moose (*Alces alces*) calves (S. D. Miller, Alaska Department of Fish and Game, unpublished data).

Survival rates of adult females were similar to rates of adult males in the Mountain Parks and SF Flathead study areas, and also similar to the 0.89–0.92 recorded for adult females in the grizzly bear reduction area of the Susitna Drainage, Alaska (S. D. Miller, Alaska Department of

Fish and Game, unpublished data). Adult female survival rates in the NF Flathead and Selkirk–Yaak, however, were similar to that of females on Chichagof Island (0.96; Titus and Beier 1994) and appeared to be higher, although not statistically so, than in the Mountain Parks and SF Flathead.

The lack of difference or perhaps even higher survival rates of adult females in some multiple-use landscapes (e.g., NF Flathead, Selkirk–Yaak) compared to areas dominated by protected areas (e.g., Mountain Parks) is an important consideration in developing conservation strategies. Although few radiocollared grizzly bears died when inside park boundaries, grizzly bears had high mortality rates on the periphery. The high mortality rate along park boundaries is likely an indirect result of nearly 1 million people (i.e., Calgary metropolitan area) within a 1–2-hr drive, and approximately 43,000 residents and 28,000 hotel beds in occupied grizzly bear habitat of the Mountain Park study areas. Similarly, within the SF Flathead study area, Mace and Waller (1998) found that grizzly bears with home ranges entirely within multiple-use areas had higher survival rates than grizzly bears that also used rural settlements or designated wilderness areas. We suggest that the long-term conservation value of protected areas is not only related to the amount and quality of habitat they contain and their grizzly bear management programs, but also the number and activities of people using the protected area and adjacent lands. Multiple-use lands remote from human population centers may be critical to the long-term conservation of grizzly bears, provided that they are managed for low-density human use.

Most radiocollared grizzly bears died because people killed them. Hunting was a significant factor only in British Columbia, where it accounted for less than half the deaths. In more remote areas, a higher proportion of grizzly bear deaths probably would be from legal hunting because, with less human settlement, control killing would be reduced (Miller and Chihuly 1987). Results from remote study areas in Alaska suggest that between 78 and 100% of the human-caused deaths of radiocollared grizzly bears were from hunting (Schoen and Beier 1990, Reynolds 1993, Sellers 1994).

Biases

Using radiocollared bears to estimate survival rates and causes of death has potential biases. First, study areas were not located randomly. To obtain sufficient sample sizes, telemetry studies were sometimes located in or at least included areas where grizzly bears were relatively abundant and human influences less common. The NF Flathead and SF Flathead studies, which together contributed about half of the data, had little human settlement. Although a large proportion of grizzly bears likely lives in similar unsettled valleys, it is probable that grizzly bears in unsettled areas have higher survival rates and are legally shot by hunters or die naturally more often than grizzly bears that live closer to people.

A second potential bias of using radiocollared grizzly bears is that people may be less likely to shoot radiocollared grizzly bears but more likely to report the radiocollared grizzly bears that they do shoot. Radiocollars used were black or brown and were difficult to see on a living grizzly bear; however, some hunters or poachers may have avoided killing radiocollared grizzly bears. Due to these biases, it is likely that actual survival rates were less than reported here, and even a higher proportion of deaths were unknown to management agencies.

Finally, pooling data from several studies will weigh areas and time periods unequally; thus, results may not be representative of the entire study area group. The Mountain Parks study area group contained data from 6 studies, each with insufficient data to test if pooling was justified. Because most data came from 2 geographically large and recent projects (Eastern Slopes, Upper Columbia) and management goals have remained the same over the duration of all studies, we believe the data are representative of the area.

MANAGEMENT IMPLICATIONS

Reducing or controlling grizzly bear mortality is central to grizzly bear management in the southern extreme of their distribution. Managers must not only understand why grizzly bears are being killed, but what proportion of deaths is detected. Undetected deaths were usually due to nonhunting human causes. Development and implementation of comprehensive access, recreation, and settlement plans is essential in occupied grizzly bear habitat to maintain a low density of people, particularly those who engage in activities that put grizzly bears at risk (McLellan 1990, Mattson et al. 1996, Mace and Waller 1997*a*).

Black bear and ungulate hunters killed a relatively high proportion of the radiocollared grizzly bears. Misidentification, self-defense, and problems associated with attractants such as garbage, food, and ungulate carcasses in hunting camps were often the reason for killing grizzly bears. Enforcement of existing rules on clean camping and stressing techniques for hunting in grizzly bear country during hunter training courses and in regulation synopses may reduce the number of grizzly bear mortalities associated with big game hunting seasons.

Managers should incorporate appropriate estimates of unreported kills in estimates of acceptable harvest rates. These estimates, however, remain uncertain but appear to depend on the amount of legal hunting and the degree that grizzly bears and people share habitat. In remote areas with legal hunting, managers will likely be aware of >70% of the grizzly bears killed by people. In areas without legal hunting and where people commonly live, work, and recreate in occupied grizzly bear habitat, the unreported number of bears that people kill is likely similar to the number reported.

Protected areas that are close to large human population centers may not always be suitable cores for grizzly bear conservation. Such protected areas may require intensive management of recreation, industry, and human settlement along their periphery to ensure long-term viability of local grizzly bear populations. The importance of well-managed multiple-use land should be recognized during conservation planning processes. If land-use plans for multiple-use areas can ensure no human settlement and low levels of recreational activity, then these areas may serve as source populations.

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