Demographics and population trends of grizzly bears in the Cabinet–Yaak and Selkirk Ecosystems of British Columbia, Idaho, Montana, and Washington

Wayne L. Wakkinen[1,3] and Wayne F. Kasworm[2,4]

[1]*Idaho Department of Fish and Game, HCR 85 Box 323J, Bonners Ferry, ID 83805, USA*
[2]*U.S. Fish and Wildlife Service, 475 Fish Hatchery Road, Libby, MT 59923, USA*

Abstract: We summarize and report survival and cause-specific mortality of grizzly bears in the Cabinet–Yaak and Selkirk Mountains recovery zones from 1983–2002 to examine effects on the populations. Fifty-four percent of total known mortality in the Cabinet–Yaak was human-caused ($n =$ 28) and 80% of total known mortality in the Selkirk Mountains was human-caused ($n = 40$). We investigated demographic values of 53 and 61 radiocollared grizzly bears (*Ursus arctos*) and attendant offspring in the Cabinet–Yaak and Selkirk Mountains recovery zones, respectively from 1983–2002. Nineteen mortalities of radiocollared animals or offspring were detected in the Cabinet–Yaak sample and 20 in the Selkirk Mountains. Estimated survival rates were 0.929 (95% CI = 0.091) for adult females, 0.847 (95% CI = 0.153) for adult males, 0.771 (95% CI = 0.208) for subadult females, 0.750 (95% CI = 0.520) for subadult males, 0.875 (95% CI = 0.231) for yearlings, and 0.679 (95% CI = 0.179) for cubs in the Cabinet–Yaak. Estimated survival rates for the Selkirk Mountains were 0.936 (95% CI = 0.064) for adult females, 0.908 (95% CI = 0.102) for adult males, 0.900 (95% CI = 0.197) for subadult females, 0.765 (95% CI = 0.176) for subadult males, 0.784 (95% CI = 0.178) for yearlings, and 0.875 (95% CI = 0.125) for cubs. Reproductive rates were 0.291 and 0.284 female cubs/year/adult female for the Cabinet–Yaak and Selkirk Mountains recovery zones, respectfully. The annual exponential rate of increase (r) was –0.037 for the Cabinet–Yaak recovery zone and 0.018 for the Selkirk Mountains.

Key words: British Columbia, Cabinet–Yaak, grizzly bear, Idaho, Montana, mortality, population trend, reproduction, Selkirks, survival, *Ursus arctos*, Washington

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Grizzly bears once existed throughout the central and western U.S. (U.S. Fish and Wildlife Service 1993). Today, grizzly bears within the contiguous states are restricted to 1–2% of their former range and exist in only 5 areas, including the Greater Yellowstone Ecosystem, Glacier National Park and the northern continental divide, and portions of northwestern Montana, northern Idaho, and northeastern and north central Washington.

Grizzly bears were listed as threatened under the Endangered Species Act (U.S. Code 1531–1544) in 1975. Active research began in both the Cabinet–Yaak and Selkirk recovery zones in 1983 when one bear was captured and radiocollared in each ecosystem. Knick and Kasworm (1989) and later Wielgus et al. (1994) reported that human-caused mortalities were taking an excessive toll on radiomarked grizzly bears at that time. Reports from other recovery zones have confirmed human-caused mortalities as a major inhibiting factor in grizzly bear recovery efforts. Research has continued in both recovery zones. In this paper we revisit the issue of human-caused mortalities in these recovery zones with additional data. Further, we use radio telemetry data to estimate survival rates, cause-specific mortality rates, and a population trend estimate for each area. Implications of the findings are discussed as they affect recovery efforts.

Study area

Population characteristics of grizzly bears were studied from 1983–2002 in the Cabinet–Yaak ecosystem of northwest Montana (48°N, 116°W) and the Selkirk Mountains ecosystem of northern Idaho, northeastern

[3]wakkinen@coldreams.com [4]Wayne_Kasworm@fws.gov

Washington, and southern British Columbia (49°N, 117°W).

The Cabinet–Yaak ecosystem encompasses approximately 2,600 km^2 in the Yaak River drainage and 4,200 km^2 in the Cabinet Mountains. The ecosystem is bisected by the Kootenai River, with the Cabinet Mountains to the south and the Yaak River area to the north. Approximately 90% of the study area is on public land administered by the Kootenai and Panhandle National Forests. The Cabinet Mountains Wilderness Area encompasses 381 km^2 of the study area at higher elevations of the Cabinet Mountains. Road density in this study area varies from 0 km/km^2 within the Wilderness Area to as high as 3 km/km^2 on corporate timberlands. Elevation on this study area ranges from 664 m along the Kootenai River to 2,664 m at Snowshoe Peak.

The Selkirk Mountains ecosystem includes 5,700 km^2 of northeastern Washington, northern Idaho, and southern British Columbia (BC). Approximately 2,700 km^2 of this area is in BC. Elevation for the area ranges from 540 to 2,375 m with a trend toward lower mean elevations in the southern portion of the ecosystem. The Selkirk ecosystem is fairly well defined by geographical boundaries and includes the Selkirk Mountains bounded by Kootenay Lake and the Kootenai River on the north and east and the Salmo and Pend Oreille rivers on the west and south.

Weather is dominated by a Pacific maritime climate characterized by short, warm summers and heavy, wet winter snowfalls. Annual precipitation averages >250 cm with winter snowfall >700 cm at higher elevations (Krajina 1967). South and west slopes at lower elevations supported stands of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) dominated the lower elevation moist sites. Mixed stands of subalpine fir (*Abies lasiocarpa*), spruce (*Picea engelmannii*), and mountain hemlock (*Tsuga mertensiana*) were predominant above 1,500 m. Lodgepole pine (*Pinus contorta*) dominated large areas at mid and upper elevations, especially north of the Kootenai River in the Yaak Mountains. Mixed stands of coniferous and deciduous trees were interspersed with riparian shrubfields and wet meadows along the major rivers. Huckleberry (*Vaccinium* spp.), an important food for grizzly and black bears (*Ursus americanus*), was a common component in the understory. The occurrence of huckleberry and other berry-producing shrubs was largely a result of wildfires that occurred between 1910 and 1929, and more recently from timber harvest activities. Effective fire suppression greatly reduced wildfire as a natural force in creating and maintaining berry-producing shrubfields. However, 2 large wildfires in the Selkirk ecosystem burned approximately 15,000 hectares in 1967 and resulted in large early-seral shrubfields. Fires of this size are currently the exception rather than the norm.

High, precipitous peaks with steep slopes characterize the Cabinet Mountains. The Yaak River drainage to the north is lower in elevation, has gentler slopes, and is more forest-covered. Conversely, in the Selkirks the higher, steeper mountains are found in the northern portion of the study area while the south contains lower, gentler slopes. Contemporary resource use included mineral exploration and extraction, timber harvest, and recreation.

Methods

Capture and marking

Bears were captured for research purposes with leg-hold snares following the techniques described by Johnson and Pelton (1980). A trap-night was defined as one trap site set with one or more leg-hold snares. Immobilized bears were measured, weighed, and tattooed, and a first premolar tooth was extracted for age determination (Stoneberg and Jonkel 1966). Captured bears were assigned to 6 classes based on age and sex: adult (≥5 years old) males and females, subadult (2–4 years old) males and females, yearlings (1 year old), and cubs (<1 year old).

Each captured bear was marked with individually numbered ear tags. Captured bears were fitted with motion-sensitive radiocollars or ear-tag transmitters. Ear-tag transmitters allowed us to mark small bears, such as yearlings. Cubs were typically ear-tagged and released. A canvas spacer in each collar was designed to allow the collar to drop off in 2–3 years (Hellgren et al. 1988). Trapping efforts were conducted in the Cabinet–Yaak ecosystem from May through September and in the Selkirks from May through August in 1983–2002. Trap sites were typically located within 200 m of a road to allow vehicle access. In the Selkirks, most of the trapping was done on roads closed to public motorized traffic. In the Cabinet–Yaak study area, trapping occurred on both open and closed roads. Additionally, some trapping in remote areas was accomplished with the use of pack-stock.

Radiomonitoring

Instrumented bears were aerially located each week (weather permitting) during the 6–8 month period in which they were active. Collars that were inactive for unusual periods of time or had mortality signals were approached from the ground and a determination made of the fate of the bear.

Total known mortality

Mortality records from each recovery zone were examined and classified by sex, age, season of occurrence, and mortality cause from 1983–2002. Mortality categories included defense of life, legal hunting, management removal, mistaken identity, natural, poaching, research, train collision, unknown but human-caused, and unknown. Cubs that disappeared during their first year of life when their mother was known to survive were assumed to have died from natural causes. Deaths of bears found with parts removed (e.g. claws) were classified as poaching. A bear killed as a direct result of activities associated with our trapping and research efforts was classified as a research mortality. Bears that were shot but for which we could not determine the circumstances of their death were classified as "unknown/human-caused" as were retrievals of cut off radiocollars where no carcass was discovered. Total known mortalities include all known grizzly bear deaths and are not restricted to radiocollared animals.

Survival rate estimation

Survival rates for all age classes except cubs were calculated by use of the Kaplan-Meier procedure as modified for staggered entry of animals (Pollock et al. 1989). Assumptions of this method include the following: marked individuals were representative of the population, individuals had independent probabilities of survival, capture and radiocollaring did not affect future survival, censoring mechanisms were random, an initial time of monitoring could be defined, and newly collared animals had the same survival function as previously collared animals. Censoring was defined as radiocollared animals lost due to radio failure, radio loss, or emigration of the animal from the study area.

Our time origin for each bear began at the time of capture. If a bear changed age classification when it was radiocollared, (i.e., subadult to adult), the change in status occurred on the first of February, which was the assigned birth date of all bears. Weeks were used as the interval in the Kaplan-Meier procedure during which survival rates were assumed constant. No mortality was observed during the denning season. Animals were intermittently added to the sample over the 20 years of the study.

Mortality dates were established based on radio telemetry, collar retrieval, and mortality site inspection. Radio failure dates were estimated using the date of the last radiolocation when the animal was known to be alive.

Cub survival rates were estimated by 1 − (cub mortalities/total cubs observed), based on observations of radiocollared females (Hovey and McLellan 1996). Mortality was assumed when a cub disappeared or the mother died. This method was used because cubs are rarely radiocollared and their mortality often occurs early in the year.

Only bears captured as part of this research effort were included in survival calculations. Bears trapped for specific management purposes (e.g., prior history of nuisance activity) were not included. Research bears that subsequently got into a management situation remained part of the analysis. Bears captured and relocated to the Cabinet Mountains as a test of population augmentation (Kasworm et al. 1998) and 3 yearling bears captured as part of a preemptive move to avoid nuisance activity were included in the sample. None of these animals had any prior history of nuisance activity.

Reproduction

Reproduction data were gathered through observations of radiocollared females with attendant offspring. Because of the possible undocumented neonatal loss of cubs-of-the-year, no determination of litter size was made if an observation of the radiocollared female was made in the summer or fall. Interbirth interval was defined as the length of time between subsequent births if the offspring lived at least one year. If cubs were produced but lost in the first year, that year was included in any determination of interbirth interval for subsequent years. In 3 cases adult females of reproductive age were not documented with offspring during the period they were radiocollared despite evidence of past reproduction. This could have been due to undetected neonatal losses. Rather than censor these cases from the database and thus lose those data, we added the average interbirth interval of bears with known intervals to the number of years that the bear was observed without offspring to assign a conservatively estimated interbirth interval. In all 3 cases the females were observed for 2 years. The average interbirth interval for other bears with known complete interbirth intervals was 3 years; therefore, these females were assigned an interbirth interval of 5 years. In another case, a 20-year-old female was observed with two 2-year-old offspring but was not observed with cubs for 2 subsequent years, at which point her collar failed. She was assigned an interbirth interval of 5 years for this last period. No litter size was recorded in the database for these cases. Age of first parturition was calculated using techniques described by Garshelis et al. (1998). Presence or lack of cubs was determined by visual observations of known-age radiocollared females or measurements and coloration of mammary glands at capture.

Population growth rate

We used the software program Booter 1.0 (F. Hovey, Simon Fraser University, Burnaby, B.C.) to estimate the finite rate of increase (lambda [λ]) for the study area's grizzly bear populations. The estimate of λ was based on adult and subadult female survival, yearling and cub survival, age at first parturition, reproductive rate, and maximum age of reproduction.

Booter uses the following revised Lotka equation (Hovey and McLellan 1996), which assumes a stable age distribution:

$$0 = \lambda^a - S_a\lambda^{a-1} - S_cS_yS_s^{a-2}m[1 - (S_a/\lambda)^{w-a+1}] \quad (1)$$

where S_a, S_s, S_y, and S_c are adult female, subadult female, yearling, and cub survival rates, respectively, $a =$ age of first parturition, $m =$ rate of reproduction, and $w =$ maximum age. Booter internally calculates annual survival rates with a seasonal hazard function estimated from censored telemetry information collected through all years of monitoring for use in its calculation of λ. This calculation may result in point estimates and confidence intervals slightly different from those produced by Kaplan-Meier techniques (see differences between Tables 2 and 3). The survival rate for each class was calculated as:

$$S_i = \prod_{j=1}^{k} e^{-L_j(D_{ij}-T_{ij})} \quad (2)$$

where S_i is survival of age class i, k is the number of seasons, D_{ij} is the number of recorded deaths for age class i in season j, T_{ij} is the number of days observed by radio telemetry, and L_j is the length of season j in days. Cub survival rates were estimated by 1 − (cub mortalities/total cubs born), based on observations of radiocollared females. Intervals were based on seasons defined as: spring (1 Apr–31 May), summer (1 Jun–31 Aug), fall (1 Sep–30 Nov), and winter (1 Dec–31 Mar). Survival rates were assumed constant during these intervals and corresponded with spring and fall hunting seasons and the denning season.

Booter provides the option of using paired or unpaired reproductive data to calculate a reproductive rate (m). If paired data are selected, only bears with known litter size and interbirth interval are used. With our data, this option appeared to bias the results because the paired sample documented shorter interbirth intervals, thereby artificially inflating the true population reproductive rate (using this option: Cabinet–Yaak $m = 0.378$; Selkirk $m =$ 0.414). We selected the option of using unpaired data with sample size restricted to the number of females. This allows the use of bears with known interbirth intervals but unknown litter sizes and bears with known litter size but unknown intervals due to radio failure or death. To calculate reproductive rates, the following formula was used (from Booter 1.0):

$$m = \frac{\sum_{i=1}^{n} \frac{\sum_{j=1}^{p} L_{ij}}{\sum_{j=1}^{k} B_{ij}}}{n} \quad (3)$$

where $n =$ number of females; $j =$ observations of litter size (L) or interbirth interval (B) for female i; $p =$ number of observations of L for female i; and $k =$ number of observations of B for female i. Values for k and p may not be equal. Sex ratio of cubs was assumed to be 1:1, and maximum age of female reproduction (w) was set at 27 years (Schwartz et al. 2003). The average annual exponential rate of increase was calculated as $r = \log_e \lambda$ (Caughley 1977).

Results

Cabinet–Yaak grizzly bear captures and trap success

Captures and trap success varied dramatically between study areas in the Cabinet–Yaak recovery zone. Three different grizzly bears were captured in the Cabinet Mountains by research efforts during 5,884 trap-nights from 1983 to 2002. Three additional grizzly bears were captured in 2002 as part of a preemptive move away from human inhabited areas. Twenty-six individual grizzly bears were captured in the Yaak River area during 5,763 trap-nights from 1986 to 2002. Capture success in the Cabinet Mountains (1 bear/1,961 trap-nights) was approximately one-tenth that in the Yaak River (1 bear/ 222 trap-nights).

Thirty-two grizzly bears were captured in the Cabinet–Yaak recovery zone as part of research efforts. Four female and 12 male grizzly bears 5–21 years-old and 10 female and 6 male bears $\leq$4 years old were radiocollared. Eighteen additional cub or yearling bears were monitored as the attendant offspring of radiocollared females. Individual bears were monitored for 0.25–10.25 years. No radiocollared grizzly bears in the Cabinet–Yaak recovery zone that were captured for this research effort later became management bears during the study period.

Selkirk grizzly bear captures and trap success

Trapping was conducted in both the U.S. and BC portion of the ecosystem. Sixty-one grizzly bears were trapped from 1983 to 2002 in 2,921 trap-nights. Capture rates varied between the U.S. and BC portions of the ecosystem. Thirty-eight individual grizzly bears were captured in the U.S. portion of the recovery zone in 2,443 trap-nights from 1983 to 2002. Twenty-three individual grizzly bears were captured in the BC portion of the recovery zone in 478 trap-nights from 1985 to 1999. The capture rate in BC (21 trap-nights/bear capture) was approximately 3 times higher than the capture rate in the U.S. portion of the ecosystem (64 trap-nights/bear capture).

Eighteen females and 18 males ranging from 5 to over 25 years of age and 9 females and 16 males $\leq$4 years old were fitted with radiocollars. Thirty-one additional cub or yearling attendant offspring were also monitored. Individual bears carried functional radiocollars from 0.02 to 10.41 years. One subadult male grizzly bear that was captured as part of the research effort became a management bear and was removed from the ecosystem during the study period. This bear was monitored for 0.97 bear-years.

Cabinet–Yaak total known mortality

Twenty-seven instances of grizzly bear mortality were detected inside or within 16 km of the Cabinet–Yaak recovery zone during 1983–2002 (Table 1). Three adult females, 3 adult males, 4 female subadults, 2 male subadults, 2 female yearlings, and 1 female cub were included in the known sex and age individuals. Mortality cause frequency in descending order was natural (12), defense (3), mistaken identity (3), unknown but human-caused (3), poaching (2), management removal (1), research (1), train collision (1), and unknown (1). Nine mortalities occurred during spring, 8 during fall, and 6 during summer. Seven of 12 natural mortalities occurred during spring and 5 occurred during summer. Two unknown but human-caused mortalities occurred during fall and 1 occurred during spring. All 3 defense of life instances occurred during fall. One mistaken-identity mortality occurred during spring, 1 in fall, and 1 in an unknown season. Season of occurrence was unknown for 3 poaching mortalities.

The public reported 11 of 27 (41%) total mortality incidents and 10 of 14 (71%) human-caused mortalities to management authorities. Other mortality was discovered by agency personnel or with the aid of radio telemetry. Ten of 13 (77%) known-location human-caused mortalities occurred <500 m of a road open to public travel. Twelve instances of known mortality occurred during the 16 years of 1983–1998; however, 15 instances of known mortality occurred during 1999–2002. Eight of the 12 (75%) mortalities occurring during 1983–1998 were human-caused, as were 6 of 15 (40%) during 1999–2002. Rates of human-caused mortality were 0.50 mortalities/year in 1983–1998 and 1.50 mortalities/year in 1999–2002.

Selkirk total known mortality

Forty grizzly bear mortalities were detected within 16 km of the Selkirk recovery zone from 1983–2002 (Table 1), including 6 adult females, 6 adult males, 2 subadult females, 6 subadult males, 2 yearling females, and 2 yearling males. Additionally, 8 males of unknown age and 4 cubs and 4 yearlings of unknown sex are included in this total. Mortality cause, in descending order, was human-caused but unknown circumstances (11), management removal (9), natural (7), poaching (6), hunting (3), and mistaken identity (2). Self-defense and an unknown mortality each accounted for one death. Seven mortalities occurred in the spring, 6 in the summer, and 21 in the fall. Season of death was unknown for 6 bears. Two unknown but human-caused deaths occurred in spring, 2 in summer, and 7 in fall. Five of 9 management removals were in fall and 1 was in summer; the timing of 3 removals was not recorded. Three natural mortalities were in summer, 1 in fall, and 3 were unknown. Five of 6 poachings occurred in fall with the remaining death in spring. All legal hunting deaths occurred in spring. Both mistaken identity deaths occurred in fall. The unknown mortality occurred in summer and the defense of life kill occurred in fall.

Fifteen of 32 human-caused deaths (42%) were reported to management authorities by the public. Other mortality was discovered by agency personnel or with the aid of radio telemetry. Nineteen of 25 (76%) known location human-caused mortalities occurred <500 m of a road open to public travel. For 1983–2002, total known mortalities averaged 2.0/year and known human-caused deaths averaged 1.6/year.

Cabinet–Yaak survival and cause-specific mortality

Survival and cause-specific mortality rates were calculated for 6 sex and age classes of bears (Table 2). Adult female survival was 0.929 (95% CI = 0.838–1.019) with 2 instances of natural mortality among 9 radiocollared bears monitored for 28.7 years. Both natural mortalities occurred during summer. Adult male survival was 0.847 (95% CI = 0.694–1.000), with 1 hunting mortality, 1 defense of life, and 1 unknown

Table 1. Causes and timing of known grizzly bear mortalities in or within 10 miles of the Cabinet–Yaak (CY) and Selkirk Mountains (SM) recovery zones, 1983–2002. Numbers within parentheses indicate mortalities for the CY and SM recovery zones, respectively. Cells with no entry indicate no known mortalities.

	Mortality cause										
Category	Defense of life	Hunting	Management removal	Mistaken identity	Natural	Poaching	Research	Train collision	Unknown, human	Unknown	Total
Adult female	2 (1,1)				5 (2,3)	1 (0,1)			1 (0,1)		9 (3,6)
Subadult female	1 (1,0)			1 (0,1)		1 (0,1)	1 (1,0)		2 (2,0)		6 (4,2)
Adult male	1 (1,0)		3 (1,2)			3 (1,2)			1 (0,1)	1 (0,1)	9 (3,6)
Subadult male			1 (0,1)	1 (0,1)		1 (1,0)			5 (1,4)		8 (2,6)
Unknown male		3 (0,3)	5 (0,5)								8 (0,8)
Yearling			1 (0,1)	1 (1,0)	3 (1,2)				5 (0,5)		10 (2,8)
Cub				1 (1,0)	11 (9,2)	2 (0,2)					14 (10,4)
Unknown				1 (1,0)				1 (1,0)		1 (1,0)	3 (3,0)
Total	4 (3,1)	3 (0,3)	10 (1,9)	5 (3,2)	19 (12,7)	8 (2,6)	1 (1,0)	1 (1,0)	14 (3,11)	2 (1,1)	67 (27,40)
Spring[a]		3 (0,3)		1 (1,0)	7 (7,0)	1 (0,1)			3 (1,2)	1 (0,1)	16 (9,7)
Summer[b]			1 (0,1)		8 (5,3)		1 (1,0)		2 (0,2)		12 (6,6)
Autumn[c]	4 (3,1)		6 (1,5)	3 (1,2)	1 (0,1)	5 (0,5)		1 (1,0)	9 (2,7)		29 (8,21)
Unknown			3 (0,3)	1 (1,0)	3 (0,3)	2 (2,0)				1 (1,0)	10 (4,6)

[a]Spring = 1 Apr–31 May.
[b]Summer = 1 Jun–31 Aug.
[c]Autumn = 1 Sep–30 Nov.

but human-caused mortality among 13 radiocollared bears monitored for 19.0 years. The hunting mortality occurred during spring 35 km northwest of the recovery zone in British Columbia. The defense of life and the unknown but human-caused mortality occurred during fall. Subadult female survival was 0.771 (95% CI = 0.563–0.980) among 10 bears monitored for 12.6 years. A research mortality occurred in summer when a bear captured in a foot snare was killed by another grizzly bear. A defense of life and an unknown but human-caused mortality occurred during fall.

Four subadult males were monitored for 3.1 years and had a survival rate of 0.750 (95% CI = 0.230–1.270). There was 1 spring unknown but human-caused mortality. Yearling survival was 0.875 (95% CI = 0.661–1.089) among 17 bears monitored for 9.2 years. One bear died during summer from natural causes. Nine of 28 cubs died resulting in a survival rate of 0.679 (95% CI = 0.500–0.857). All cubs were believed to have died of natural causes, 2 during spring and 7 during summer.

Selkirk survival and cause-specific mortality

Survival and cause-specific mortality rates were calculated for 6 sex and age classes of bears (Table 2). Adult female survival was 0.936 (95% CI = 0.872–0.999) with 3 instances of natural mortality and 1 case of poaching among 20 radiocollared bears monitored for 54.9 years. All natural mortalities occurred during summer and the case of poaching occurred in fall. Adult male survival was 0.908 (95% CI = 0.806–1.010) with 2 poaching mortalities and 1 unknown cause of death among 19 radiocollared bears monitored for 28.0 years. One poaching occurred in spring and one in fall. The unknown mortality occurred in the summer.

Subadult female survival was 0.900 (95% CI = 0.703–1.097) with one case of mistaken identity among 7 bears monitored for 5.5 years. The mistaken identity kill occurred in fall. Twelve subadult males were monitored for 15.0 years and produced a survival rate of 0.765 (95% CI = 0.589–0.942). Mortalities included a mistaken identity kill in fall, a poaching kill in spring, and 2 unknown but human caused mortalities, 1 in summer and 1 in fall. Yearling survival was 0.784 (95% CI = 0.606–0.963) among 22 bears monitored for 16.6 years. Three bears died of natural causes, one each in spring, summer, and fall. There was one case of an unknown-but human-caused death in fall. Four of 32 monitored cubs died, resulting in a survival rate of 0.875 (95% CI = 0.750–1.000). Two of the deaths were cubs

Table 2. Survival and cause-specific mortality rates of grizzly bear sex and age classes based on censored telemetry data in the Cabinet–Yaak and Selkirk Mountains recovery zones, 1983–2002.

	Demographic parameters and mortality rates					
Area parameter	**Adult male**	**Adult female**	**Subadult male**	**Subadult female**	**Yearling**	**Cub**
Cabinet–Yaak						
Individuals/bear-years	13/19.0	9/28.7	4/3.1	10/12.6	17/9.2	28/28[a]
Survival[b] (95% CI)	0.847 (0.694–1.0)	0.929 (0.838–1.0)	0.750 (0.230–1.0)	0.771 (0.563–0.980)	0.875 (0.661–1.0)	0.679 (0.500–0.857)
Mortality cause						
Hunting	0.059	0	0	0	0	0
Natural	0	0.071	0	0	0.125	0.321
Defense of life	0.047	0	0	0.064	0	0
Research	0	0	0	0.100	0	0
Unknown	0.047	0	0.250	0.064	0	0
Selkirk Mountains						
Individuals/bear-years	19/28.0	20/54.9	12/15.0	7/5.5	22/16.6	32/32[a]
Survival[b] (95% CI)	0.908 (0.806–1.0)	0.936 (0.872–0.999)	0.765 (0.589–0.942)	0.900 (0.703–1.0)	0.784 (0.606–0.963)	0.875 (0.750–0.969)
Mortality cause						
Mistaken identity	0	0	0.039	0.100	0	0
Natural	0	0.048	0	0	0.162	0.125
Poaching	0.061	0.016	0.078	0	0	0
Human, unknown	0	0	0.118	0	0.054	0
Unknown	0.031	0	0	0	0	0

[a]Cub survival based on counts of individuals alive and dead.
[b]Kaplan-Meier survival estimate.

assumed to be dead when the mother died. The other 2 deaths were natural and occurred in summer.

Cabinet–Yaak reproduction

Fourteen litters comprised of 29 cubs were observed through monitoring radiocollared bears, for a mean litter size of 2.07 (95% CI = 1.80–2.35). Three radiocollared adult female bears provided 7 complete interbirth intervals. Mean interbirth interval was 3.0 years (95% CI = 1.9–4.1). Two successive instances of a female losing a complete litter of cubs prior to breeding season and producing another litter the following year were observed. Sex ratio of bears captured as cubs or yearlings was 8 females:5 males. Estimated reproductive rate was 0.287 female cubs/year/adult female (95% CI = 0.192–0.464). Age of first parturition was 6.6 years (95% CI = 5.9–7.3, $n = 5$).

Selkirk reproduction

Seventeen litters comprised of 37 cubs were observed through monitoring radiocollared bears for a mean litter size of 2.18 (95% CI = 1.93–2.43). Six radiocollared adult female bears provided 8 complete interbirth intervals for a mean interval length of 3.0. Three other bears were assigned an estimated interbirth interval. Including these bears, the mean population interbirth interval was an estimated 3.5 years (95% CI = 2.8–4.3). Sex ratio of bears captured as cubs or yearlings was 3 females and 4 males. Estimated reproductive rate was 0.288 female cubs/year/adult female (95% CI = 0.235–0.362). Age of first parturition was 6.5 years old (95% CI = 6.1–6.9, $n = 8$).

Cabinet–Yaak population trend

The estimated finite rate of increase (λ) for 1983–2002 was 0.964 (95% CI = 0.844–1.063) based on the estimated demographic variables (Table 3). Subadult female survival accounted for most (58.2%) of the uncertainty in λ, with adult female survival (28.2%), reproductive rate (7.7%), yearling survival (3.5%), cub survival (2.2%), and age at first parturition (0.4%) contributing much smaller amounts. The probability that the population was declining ($\lambda < 1.0$) was 75.1%. The annual exponential rate of increase (r) was –0.037.

Selkirk population trend

The estimated finite rate of increase (λ) was 1.019 (95% CI = 0.922–1.098) based on the estimated demographic variables (Table 3). Subadult female survival accounted for most (75.3%) of the uncertainty in λ, with adult female survival (15.7%), yearling survival (4.3%), reproductive rate (3.3%), cub survival

Table 3. Estimated annual survival rates, age at first parturition, reproductive rates, and population trend of grizzly bears in the Cabinet–Yaak and Selkirk Mountains recovery zones, 1983–2002.

Area parameter	Sample size	Estimate (95% CI)	SE	Variance (%)[a]
Cabinet–Yaak				
Adult female survival[b] (S_a)	9/28.7[c]	0.926 (0.810–1.0)	0.050	28.1
Subadult female survival[b] (S_s)	10/12.6[c]	0.781 (0.535–1.0)	0.114	58.9
Yearling survival[b] (S_y)	17/9.2[c]	0.851 (0.540–1.0)	0.139	3.5
Cub survival[b] (S_c)[d]	28/28	0.679 (0.500–0.857)	0.090	2.3
Age first parturition (a)	5	6.6 (6.2–7.0)	0.219	0.4
Reproductive rate (m)[e]	3/6[f]	0.287 (0.192–0.464)	0.071	7.9
Maximum age (w)	Fixed	27		
Lambda (λ)	5000 bootstrap runs	0.964 (0.849–1.063)	0.056	
Selkirk Mountains				
Adult female survival[b] (S_a)	20/54.9[c]	0.935 (0.863–0.986)	0.032	15.7
Subadult female survival[b] (S_s)	7/5.5[c]	0.878 (0.656–1.0)	0.102	75.3
Yearling survival[b] (S_y)	22/16.6[c]	0.785 (0.566–0.944)	0.100	4.3
Cub survival[b] (S_c)	32/32	0.875 (0.750–0.969)	0.059	1.2
Age first parturition (a)	8	6.5 (6.1–6.9)	0.190	0.2
Reproductive rate (m)[e]	8/12[f]	0.288 (0.235–0.362)	0.177	3.3
Maximum age (w)	Fixed	27		
Lambda (λ)	5000 bootstrap runs	1.019 (0.922–1.098)	0.046	

[a]Percent of lambda explained by each parameter.
[b]Booter survival calculation.
[c]Individuals/bear-years.
[d]Cub survival based on counts of individuals alive and dead.
[e]Number of female cubs produced/year/adult female. Sex ratio assumed to be 1:1.
[f]Sample size for birth interval/sample size for litter size.

(1.2%), and age at first parturition (0.2%) contributing much smaller amounts. The probability that the population was increasing ($\lambda > 1.0$) was 67.3%. The annual exponential rate of increase (r) was 0.018.

Discussion

Earlier survival rate estimates were made during 1983–87 for males and females regardless of age and varied from 0.53–0.86 for males and 0.89–1.0 for females in the Cabinet–Yaak and Selkirk Mountains (Knick and Kasworm 1989). Another estimate of survival rates in the Selkirk Mountains from 1983–1990 produced rates of 0.96 for adult females, 0.81 for adult males, 0.78 for subadult females, 0.90 for subadult males, and 0.84 for cubs (Wielgus et al. 1994). Yearling survival was included with subadults. Our survival point estimates for the Selkirk Mountains were generally higher for all sex and age classes except adult females and subadult males.

Comparisons of survival rates between the Cabinet–Yaak and Selkirk Mountains indicated most similarities for adult females (0.929 vs. 0.936), adult males (0.847 vs. 0.908), and subadult males (0.750 vs. 0.765), and least similarity for subadult females (0.771 vs. 0.900), yearlings (0.875 vs. 0.784), and cubs (0.679 vs. 0.875). Eberhardt (1990) concluded that adult female survival rates must be $\geq$0.90 for population growth to occur in Yellowstone populations given local reproductive rates. Survival rates of adult females reported here were within the range of rates (0.888–0.959) reported for other interior grizzly bear populations (McLellan et al. 1999). Similar relationships were noted for adult males (0.625–0.891) and subadult males (0.742–0.807). Subadult female survival rate estimates from the Cabinet–Yaak fell below the ranges of rates (0.872–0.954) reported for other interior grizzly bear populations (McLellan et al. 1999). Yearling survival rates in both our study areas fell below the range of estimates for Flathead River studies in southeast British Columbia and northwest Montana (0.900–0.944, Hovey and McLellan 1996, Mace and Waller 1998). Selkirk Mountains cub survival rates were within the range of those on Flathead and Yellowstone study areas (0.845–0.900, Eberhardt et al. 1994, Hovey and McLellan 1996, Mace and Waller 1998), but the Cabinet–Yaak cub survival estimate fell below this range.

Other reported estimates of the finite rates of population increase include: the North Fork of the Flathead River (1.085, Hovey and McLellan 1996), Yellowstone (1.046, Eberhardt et al. 1994), and the South Fork of the Flathead River (0.977, Mace and Waller

1998). Wielgus et al. (1994) reported a finite rate of increase of zero for the Selkirk Mountains during 1983–1990. The confidence intervals associated with the estimates of population increase from the Cabinet–Yaak (0.964, 95% CI = 0.844–1.063) or Selkirk Mountains (1.019, 95% CI = 0.922–1.098) do not allow us to statistically conclude that the populations were increasing or decreasing.

Rates of human and nonhuman-caused mortality in the Cabinet–Yaak appear to have increased during 1999–2002. Some of the increase of both mortality sources may be related to fluctuations in local food resources during the early part of this increase. Grizzly bears in this recovery zone are highly dependent on huckleberries for energy and fat accumulation. Huckleberry production was 50–75% of the 10-year average in this area during 1998, 1999, and 2001 (Kasworm, unpublished data). Poor food production may also cause females to travel further for food; this may expose cubs to greater risk of mortality from predators or accidents. Seven of 15 mortalities during the period involved cubs.

Another mortality involved a female with 2 cubs that appear to have been killed by another bear in 1999. A yearling female died in 2002 from natural causes (in poor condition after being orphaned when the mother was presumed killed in a train collision). Other mortality such as a management removal in 1999 may have been related to poor food production. Six of the 15 mortalities occurring from 1999 to 2002 were human caused. Self-defense, management removal, mistaken identity, and train collision were the causes of one mortality each, and 2 other bears killed by gun shot are still under investigation.

The population trend estimate using data prior to 1999 shows the effects of these recent mortalities. The estimated population increase for the Cabinet–Yaak ecosystem for 1983–1998 was 1.067 (95% CI = 0.907–1.159). Lower survival rates across most sex and age classes (particularly subadult females) and somewhat lower reproductive rates used in the computation of population trend were major factors producing the lower point estimate for 1983–2002. Reproductive rates declined largely because of litter losses that resulted in extended birth intervals. Point estimates for survival rates (from Booter calculations) of subadult females declined from 0.901 (0.672–1.000) during 1983–98 to 0.781 (0.541–1.000) during 1983–2002. Point estimates for cub survival declined from 0.867 (95% CI = 0.667–1.000) to 0.679 (95% CI = 0.500–0.857). We explored the impact of the loss of 2 subadult females to human causes in 1999 and 2000 by converting the mortalities to censors and ran the model. Under these conditions, subadult females mortality was 0.912 (0.721–1.000), and the trend estimate for the Cabinet–Yaak was 1.012 (95% CI = 0.911–1.099).

Conversely, data from the Selkirks did not show an increase in mortality and a subsequent drop in population trend during this same period. Population trend using data prior to 1999 in the Selkirks was estimated at 0.975 (95% CI = 0.861–1.092).

While the rate of human-caused mortalities in the Selkirks does not show an obvious trend, the circumstances of the mortalities do. There were 6 human-caused mortalities >500 m from an open road, and all of these occurred from 1982–93. There have been no known human-caused mortalities away from roads since, despite an emphasis on backcountry enforcement patrols to detect such mortalities and a continued presence of radiocollared grizzly bears. Conversely, mortalities near roads appear to be increasing. Twenty-five human-caused mortalities that occurred near roads were detected. Fifteen of these occurred since the last known human-caused mortality was detected away from roads in 1993. Some of these mortalities were management removals, but others were not. However, the common thread to all of but a few of these deaths is their occurrence near permanent human presence, such as houses or small communities. Management removals have been a significant cause of mortality in the Selkirk Mountains. All management removals have occurred in British Columbia, and all have been near roads. The density of grizzly bears, the proximity of people to grizzly bear habitat, the difference in legal status, or other factors may be responsible for the management removals in British Columbia.

Management implications

Human-caused mortality continues to be a significant factor affecting population growth in these recovery zones. Managers should adopt specific programs or policies including information dissemination and education, enforcement, regulation, and research designed to reduce human-caused mortalities.

Education programs for black bear (*Ursus americanus*) hunters that emphasize black bear and grizzly bear identification and behavior can reduce mistaken identity kills and defensive kills near camps or while retrieving big game carcasses in the field. The state of Montana instituted such a program in 2002, but that program need only be passed once for a hunter to purchase a black bear license. This program should be an annual requirement for black bear hunters. The states of Idaho and Washington should adopt similar programs. Information and education programs that identify ways in which campers, hunters, and residents can reduce the potential for human–bear interactions over food storage, sanitation, or other bear attractants need additional emphasis. Food storage regulations on the National Forests and National Parks are an integral part of management in the Northern Continental Divide and Yellowstone recovery zones. No food storage regulations exist in most of the Cabinet–Yaak or Selkirk Mountains recovery zones with the exception of the Colville National Forest.

Increased enforcement efforts in the form of additional patrols or contacts during the hunting season and the use of decoys could deter poaching. Decoys have been commonly used for species other than grizzly bears. The presence of information and enforcement personnel dedicated to grizzly bear management may be responsible for improved survival rates in the Selkirk Mountains. Similar personnel are needed in the Cabinet–Yaak.

Maintenance of radiocollared bears in each recovery zone has been a primary means of detecting and monitoring human-caused mortality. This program can provide a deterrent to poaching, a warning system for detection, and a means of monitoring program effectiveness.

Despite the continued influence of human-caused mortalities in the Selkirk Mountains recovery zone, the grizzly bear population appears to be expanding its range as evidenced by an increase in sightings in areas where few reports of grizzly bears previously existed (Wakkinen, unpublished data). This range expansion may also be at least partially responsible for the increase in management removals and other interactions with humans around the periphery of the recovery zone. Regardless of these gains, it must be noted that this grizzly population is still very small. Therefore, gains in recovery can quickly be reversed.

Research information from small populations of animals is typically relegated to small sample sizes, and management decisions must be based on these sparse data sets. Though point estimates of most parameters have wide confidence intervals and would not pass our standard tests of statistical rigor, they often remain our only indication of the welfare of these populations. Managers must consider this information and adopt conservative policies.

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