Some Mechanisms Underlying Variation in Vital Rates of Grizzly Bears on a Multiple Use Landscape

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ABSTRACT Understanding factors that govern the abundance of organisms is fundamental to the science of ecology and important for conservation and management of species. I used temporal and spatial comparisons to test the influence of human industrial activity, huckleberry (*Vaccinium membranaceum*) productivity, and population density on grizzly bear (*Ursus arctos*) vital rates and population trends over a 32-year period. Survival rates of adult and subadult males were 0.84 and 0.78, respectively, and lower than those of adult (0.93) or subadult females (0.96). Of the 31 bears that died while radio-collared, 26 (84%) were killed by people. Of those killed by people, 11 (35%) were legally killed by hunters and 84% were deaths that occurred <120 m from a road. In the first decade of study (1979–1988) when salvage logging and gas exploration was intensive, bear density was relatively low, and huckleberry production was generally good, the population increased ($\lambda = 1.074$) with high survival rates of cubs (0.84) and yearlings (0.86) plus a high reproductive rate of 0.374. During the second decade (1989–1998) when there was little industrial activity and huckleberry production remained good, the population continued to grow ($\lambda \approx 1.06$–1.08) because survival of all age classes remained high, but the reproductive rate declined to 0.257. Bear density reached its maximum (55.6 bears/1,000 km^2 excluding independent males) at the start of the third decade. During the third decade (1999–2010), there was little industrial activity, but huckleberry production declined dramatically and often completely failed. During the third decade the population declined ($\lambda \approx 0.955$–0.980) as the reproductive rate dropped to 0.192 because of small litters (1.82), extended interbirth intervals (2.93, 3.44, and 4.22 years in decades 1, 2, and 3, respectively) and increased age of primiparity (6.60, 7.09, and 10.46 years in decades 1, 2, and 3, respectively). Adult female survival also declined likely because more females were without offspring and thus vulnerable to hunting. The best model predicting if a parous female would have a small (0 or 1 cub) or large (2 or 3 cub) litter when not encumbered with offspring the previous mating season included both huckleberry abundance the previous year and female bear density. Population inventories during the third decade had approximately twice as many bears detected per DNA hair trap set in the portion of the valley where there had been rapid industrial development, grizzly bear hunting, and large huckleberry fields than in an adjacent portion of the valley that was protected from industry and hunting but with no major huckleberry fields. The abundance of huckleberries growing in mountains above most human activity permitted this population to expand in spite of the industrial development. The population was primarily regulated by the interaction of bear density and the density-independent production of huckleberries, their major summer-fall energy food. © 2015 The Wildlife Society.

Understanding factors that govern the abundance of organisms is fundamental to the science of ecology and important for conservation and management of species and communities (Sinclair and Krebs 2002). For large terrestrial carnivores, human-caused mortality is often a dominant factor. The extensive spatial requirements of these animals and frequent conflicts with people can lead to their death (Treves and Karanth 2003). Mortality rates are sometimes unsustainable because the life-history strategy of many apex predators emphasizes high adult survival making them particularly sensitive to additional deaths of adult females (Knight and Eberhardt 1985, McLellan 1989*a*, Schwartz et al. 2006). Within species however, density varies greatly among regions and this variation has been partly explained by food availability (Fuller et al. 1989, Hilderbrand et al. 1999, Karanth et al. 2004) indicating that bottom-up processes strongly influence populations as well.

In North America, grizzly bears (*Ursus arctos*) are a large carnivore of tenuous status, particularly towards the edge of their southern and eastern distribution (Servheen 1999). Because these bears appear sensitive to a variety of human

activities, there has been considerable effort directed towards measuring their response to people, and in particular to resource extraction industries that continue to expand across the continent. Mechanisms affecting adult mortality have become increasingly clear. Where people and grizzly bears share the landscape, >75% of bears >2 years of age are eventually killed by people (McLellan et al. 1999, Schwartz et al. 2006) and most are killed near roads and settlements (McLellan 1989b, Nielsen et al. 2004a, Schwartz et al. 2010).

For large carnivores, understating bottom-up forces is more difficult, particularly for omnivorous bears because their diet changes seasonally and includes many species of plants, insects, mammals, and fish (Mattson et al. 1991, McLellan and Hovey 1995, Munro et al. 2006). Applied researchers have relied on measuring habitat selection to help direct management towards areas bears select and are therefore assumed to be important (Waller and Mace 1997, McLellan and Hovey 2001a, Nielsen et al. 2004b, Ciarniello et al. 2007). However, habitat selection studies have provided limited understanding of the actual bottom-up mechanisms that may affect grizzly bear reproduction and survival. Because the availability and nutritional content of bear foods varies dramatically among seasons, it is uncertain which habitats or foods influence vital rates (Nielsen et al. 2010, McLellan 2011); assuming habitat selection equals importance is likely misleading (Ayers et al. 2012).

A better understanding of general, bottom-up mechanisms affecting grizzly bear populations has come from continent-wide comparisons of diets, population densities, and reproductive rates followed by more focused studies linking seasonal diets with changes in body mass or fat deposits. For example, Hilderbrand et al. (1999) demonstrated the positive relationship between the availability of spawning salmon and grizzly bear body size, litter size, and population density. Not surprisingly, a food such as salmon that is high in protein and energy yet abundantly available strongly affects populations. More focused investigations, however, found that when both salmon and berries were abundant, bears fed on both foods but mostly on berries although they are low in protein (Robbins et al. 2007). In areas without salmon but where there were sufficient high-quality vegetative foods, McLellan (2011) found bears to be small in stature but relatively fat and at higher densities than where bears focused more on obtaining terrestrial meat. These results and studies on American black bears (Ursus americanus) suggest that variation in high-energy plants also influence bottom-up processes (Rogers 1976, Elowe and Dodge 1989, Costello et al. 2003).

The initial objective of my study was to use land management as an experiment to test the hypothesis that intensive salvage logging of lodgepole pine (Pinus contorta) killed by mountain pine beetle (Dendroctonus ponderosae) plus seismic exploration and test drilling for natural gas would be harmful to a hunted grizzly bear population. I predicted that during the decade of resource development the bears would have a negative survival–fecundity rate of population increase (r_s), which is a measure of demographic vigor and indicates how well a population is coping with current conditions (Caughley 1977:54). Furthermore, this predicted negative trend would eventually lead to a lower density of bears in the developed area than in an adjacent control area without industrial activity or hunting.

I measured grizzly bear survival and reproduction over a 32-year period (1979–2010) in an area that had intensive industrial development from 1978 to 1988. In addition to the human activity, I investigated 2 other factors that may influence grizzly bear vital rates over the study period. First, the population density of grizzly bears changed, which could lead to density-dependent effects primarily on bottom-up processes (Eberhardt 1977, 2002). Second, fruit production of huckleberry (Vaccinium membranaceum) plants changed. Production varied among years but was generally good during decade 1 when industries were most active as well as during decade 2 when there was little industrial activity. The productivity of this fruit declined dramatically in the third decade when there was also little industry. Numerous papers have concluded that linking habitat selection to animal fitness is the overwhelming shortcoming of habitat evaluation studies (Garshelis 2000, Beyer et al. 2010, Nielsen et al. 2010) and that experiments to manipulate selected habitats or foods while monitoring fitness are needed (Alldredge and Griswold 2006). The change in the food that bears consume when they deposit fat required for hibernation and reproduction (McLellan 2011) provided opportunity to test the hypothesis that this energy food and the early-seral, post-fire habitats (McLellan and Hovey 2001a) where they occur limit bear populations by affecting recruitment.

I report on planned and natural experiments used to investigate mechanisms underlying both top-down (in this case, human-caused mortality) and bottom-up factors that influence grizzly bear vital rates on a multiple-use landscape. I use both temporal and spatial comparisons to test the proposed negative effects of rapid industrial development, the decline in the primary energy food in the system, and the change in bear density on vital rates of grizzly bears. While testing these main hypotheses, I also investigated the implications of hunters killing adult male grizzly bears on cub survival due to sexually selected infanticide because this has been demonstrated in Scandinavia (Swenson et al. 1997, 2001a).

STUDY AREA

The North Fork of the Flathead River begins in British Columbia (BC), Canada, and flows southward for about 65 km to where it crosses the international border into Montana, USA, at N 49° and W 114.475° and at an elevation of 1,165 m (Fig. 1). In Montana, the river forms the western boundary of Glacier National Park. Main ranges of the Rocky Mountains rise on each side of the valley to 3,000 m on the east and 2,200 m on the west. For about 20 km north and 40 km south of the border, the valley is about 10 km wide and consists of flat benches and low hills. The most intensive industrial development was on these benches and hills in BC and this area was the core of my study area.
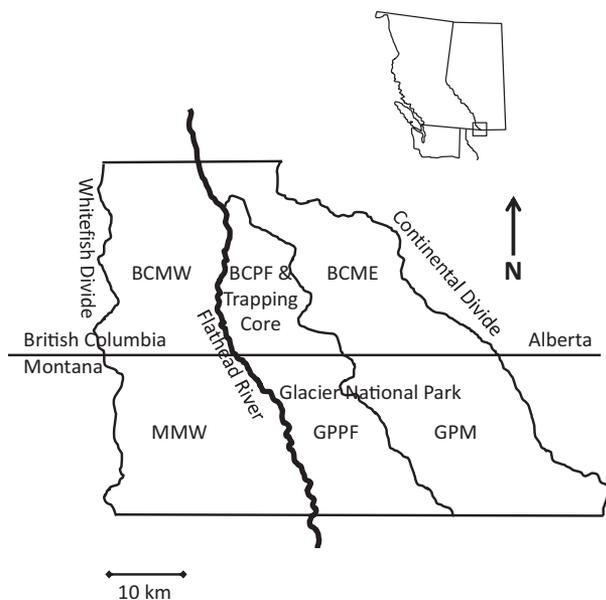
Figure 1. Study area in the extreme southeastern corner of British Columbia (BC) and adjacent part of Montana. The BC Mountains West (BCMW), BC Pine Flats (BCPF), BC Mountains East (BCME), Montana Mountains West (MMW), Glacier Park Pine Flats (GPPF), and Glacier Park Mountains (GPM) are the zones where I compared DNA hair trap visitation rates. Industrial development and grizzly bear hunting occurred in all zones in BC, but the most intensive logging and gas exploration was in the BC Pine Flats. There were major huckleberry fields in the mountains adjacent to the BC Pine Flats. The Glacier Park Pine Flats had no industry or bear hunting but no major huckleberry fields in the adjacent mountains. The core capture area was in the BC Pine Flats where a disproportionat amount of capture effort was focused.

The climate is influenced by moist Pacific Ocean air masses throughout most of the year and an average of 49 cm of precipitation/year falls in the valley at the south end of the study area (NOAA, http://www.ncdc.noaa.gov/cdo-web/datatools/normals, accessed Mar 2014). The average maximum temperature in July was 27.5°C and the average July minimum temperature was 4.9°C. In January, these temperatures were −0.5°C and −12.8°C, respectively.

Terrain, changing climate, insect outbreaks, and fire suppression have affected the fire history of the valley and thus ecological communities. There were many major stand-replacing fires between 1910 and 1930, but the 1936 fire in the BC portion of the study area was extensive and burned from valley to alpine. Huckleberry was the dominant shrub in higher-elevation burns in BC and in Montana on the west side of the valley. There were no major huckleberry fields in the western portion of Glacier National Park within 30 km of the Canadian border.

Fire suppression since 1935 likely stopped fires that would have resulted in young forests mixed among older stands (Barrett et al. 1991). The extent of older pine forests may have contributed to the scale of beetle attack in the late 1970s that was the most extensive ever recorded in the United States (Young 1988, Barrett et al. 1991). In BC, dead trees were salvage logged by clearcutting. Glacier National Park was not logged but had extensive wildfires in the summers of 1988, 2001, and 2003. In Montana, west of the Flathead

River, there was limited forest harvesting, but there were major forest fires in 1988 and 2003.

The valley in the BC part of the study area was dominated by regenerating clearcuts and logging roads among some natural forests of lodgepole pine, western larch (*Larix occidentalis*), and Douglas fir (*Pseudotsuga menziesii*). Higher elevations were also dominated by regenerating cutblocks, Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forests, slowly regenerating historical burns and avalanche chutes, rock, talus, and scree. There were no permanent residents for more than a few years and never more than 2 occupied residences at any 1 time in the BC portion of the study area.

The northwest quarter of Glacier Park was similar to north of the border except there were no clearcuts or logging roads; only 1 road goes part way through the park. There were early seral conditions from the recent forest fires in the park. West of the Flathead River and south of the border was similar to west of the river in BC except there were fewer large clearcuts in Montana. Much of the lowest elevation land along the western side of the Flathead River and major tributaries in the United States was privately owned and there were numerous permanent and seasonal residents. The Flathead valley, both north and south of the border, has a wide floodplain with rich, herb-dominated riparian areas supporting many bear foods (McLellan and Hovey 2001*a*).

The valley had a diversity of large mammals including moose (*Alces alces*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), whitetail deer (*O. virginianus*), mountain goats (*Oreaminos americanus*), and bighorn sheep (*Ovis canadensis*). Of the larger carnivores, American black bears, mountain lions (*Felis concolor*), lynx (*Felis canadensis*), and wolverine (*Gulo gulo*) were common. Wolves (*Canis lupus*) naturally recolonized the area during the study.

METHODS

Industry as the Experimental Treatment

Most industrial activity was during the first decade of study (1979–1988) and in BC. There, an average of 171,000 m³ of timber was salvage logged annually between 1978 and 1981 and then about 30,000 m³ per year until 1985 (Young 1988). Logging was followed by mechanical scarification and planting. During these years, logging camps housed between 20 and 300 people. In addition, Shell Canada Ltd. explored the Paleozoic carbonates with ground and helicopter supported seismic projects from 1980 to 1986 and drilled 9 exploratory wells between 1980 and 1990 that averaged 4,630 m deep and took 6–12 months to complete. Because of the heavy equipment and traffic, new hard-surfaced roads were built for these projects.

In BC, some forests had been harvested in the mountains in the 1960s. During my study, logging and hydrocarbon exploration continued in the mountains, but these industries were most active on the pine dominated, mostly gentle terrain between the Flathead River and the height-of-land of the first range of mountains rising above the valley to the east. This area, which I called the BC Pine Flats, covered

221 km^2, of which 22.3% was clear-cut and there were 0.74 km/km^2 of 2-wheel drive roads, 0.9 km/km^2 of smaller, more ephemeral roads, and 0.86 km/km^2 of seismic lines. Grizzly bears were legally hunted by a lottery system for a limited number of permits in BC but they were not hunted in the United States. At 1.42 bears/1,000 km^2/year, the density of hunter kills in the population unit that contains the study area was the highest in the Province (BC Government, unpublished data).

Huckleberry Production

Huckleberries are an important food for bears during the summer and fall when these animals deposit fat necessary for hibernation and reproduction (Martin 1983, Robbins et al. 2007, McLellan 2011), but, unlike most bear plant foods, productivity varies substantially among years (Martin 1983). Within the BC portion of the study area, huckleberry fruit was produced almost exclusively in higher-elevation areas that had been burned by wildfires in the 1920s and 1930s and major huckleberry shrubfields covered areas of 5–12 km^2. Each year from 1979 to 2011 (except 1995), at a minimum I surveyed the largest huckleberry shrubfield in the study area (approx. 12 km^2) along a 4-km transect starting and ending at the same location plus at least 1 other berry field. Most years I surveyed all of the largest berry fields. Along the survey, I noted the number of berries per branch and bush and then subjectively categorized production into a 5-point ordinal scale with 5 representing extremely abundant and 1 indicating virtually no berries. To ensure subjective categories reflected berry abundance, I also quantified berry production after initial categorization. In these sample areas, I counted and weighed all ripe berries in 1-m^2 circular plots at 5-m intervals along a 30-m transect. I then marked off a 15 × 30-m plot and within it I picked berries as fast as I could for 3 sequential, 10-minute sessions and weighed freshly picked berries after each session.

A lack of comparable huckleberry fields in the Glacier Park Pine Flats and Glacier Park Mountains was determined by tracking radio-collared bears in this area from both the air and ground for >30 years. A helicopter survey on 9 September 2008, when the shrubs in BC were scarlet color and easily identified, failed to find major huckleberry fields. Additionally, United States biologists who have worked on bears in this area for many years did not know of any major huckleberry fields in this area (K. Kendall, U.S. Geological Survey, personal communication; R. Mace, Montana Fish Wildlife and Parks, personal communication).

Bear Capture and Monitoring

I captured grizzly bears with foot snares or in culvert traps or darted them from a helicopter. No grizzly bears were captured because of conflicts with people. The most intensive capture program was in the core capture area located in the BC Pine Flats where industry was most active. I also captured bears in the mountains around the core area over an additional 370 km^2 where there was also industrial activity. After chemical immobilization, I removed a premolar from subadults and adults for aging and classified bears as cubs (<1 yr old), yearlings (1 yr old), subadults (2–4 yr old), and adults (>4 yr old). I attached radio collars with a canvas connector that decomposed and allowed the radio collar to drop after a planned period depending on age and sex of the bear (1–5 yr). Not only did these canvas connectors result in few neck injuries, but radio collars were usually shed when still transmitting confirming survival during the monitoring period. Observers located collared bears from fixed-wing aircraft approximately weekly from 1978 to 1995 and monthly thereafter. Between 1978 and 1992, I often tracked bears daily using ground-based methods. Observers recorded the number of cubs, yearlings and older offspring seen with radio-collared females as often as possible throughout the study.

Cause of Mortality

Radio collars contained a mortality sensor that indicated when the collar was shed or the bear had died. Observers investigated sites of suspected dead bears as soon as possible. This was usually within 2 days before 1992 but could have been up to 4 weeks after 1992. Successful grizzly bear hunters are required by law to have portions of their kill inspected so all were likely recorded. Grizzly bears killed as problem wildlife, for defense of life or property, and some illegal killing were sometimes reported to, and investigated by, conservation officers.

I first classified mortalities as natural or human-caused. I further categorized human-caused deaths by the apparent reason: 1) legal hunting; 2) defense of life or property that was either reported and legal or not reported and illegal; 3) accident, when a bear was killed by people but accidentally such as when an adult male was caught in a neck snare set for wolves; 4) poached, when the animal was hunted but killed illegally; 5) malicious, where the animal was shot and left for no apparent reason; 6) hunting violation, when a licensed hunter broke a hunting regulation, 7) illegal unknown, when the radio collar had been cut off; and 8) research, when a bear died because of handling. I recorded suspected human-caused deaths when the radio signal from a bear that had been located near human residences or camps disappeared prematurely and other evidence (i.e., blood trail) suggested the bear was killed.

Estimating Vital Rates and Population Rate of Increase

Ideally, to estimate population rate of increase assuming a stable age distribution (λ), annual survival and reproduction of females of each age would be known. Because of insufficient sample sizes, particularly for older bears, I used age-category-specific survival and reproduction of female bears. To estimate annual survival rates, I first categorized bears as cubs, yearlings, subadults, or adults.

Of the various survival estimators available, I used that of Heisey and Fuller (1985) because I was interested in cause-specific mortality rates (Heisey and Patterson 2006), it is a preferred method when mortality events are particularly common or rare (Murray 2006), it approaches the nonparametric cumulative incidence function estimator as the number of intervals increase (Heisey and Patterson 2006), plus I could combine survival with reproduction in a transparent, unified way to estimate the survival–fecundity

rate of increase. For this estimator, defining intervals appropriately is critical so I used 6 within which the daily risk of mortality was thought to remain equal (Heisey and Fuller 1985, Heisey and Patterson 2006). These intervals were based on changes in bear diet, habitat selection (McLellan and Hovey 1995, 2001a), and hunting seasons. Pre-berry with little hunting was between 15 April and 10 May, pre-berry with heavier hunting was between 11 May and 5 June, pre-berry with no hunting was 6 June to 31 July, berry season was 1 August to 20 September, post-berry with ungulate hunting was 21 September to 30 November, and winter was 1 December to 14 April.

I used only bears with functioning radio collars to estimate survival rates. When bears dropped their collars or collars expired, I censored the individual on the last day it carried a functioning collar. For each individual, I recorded the number of days it was tracked each interval, which provided the number of days it was at risk. I also recorded whether or not the bear died during that interval while still wearing a functioning radio collar. I resampled records for individuals with replacement (bootstrapped) until the number of cases in the resample equaled the number of individuals with records using the Microsoft Excel (Microsoft, Redmond, WA) add-in program PopTools (Hood 2008). For each resample, I calculated the daily survival rate per interval by the total number of days bears were at risk (i.e., survival monitored) minus the number of bears that died during that interval, divided by the total number of days at risk. I raised this daily rate to the power of the number of days in the interval to determine its contribution to the annual rate. The annual survival rate was the product of all interval rates. I estimated sex and cause-specific mortality rates for legal hunting, human-causes other than legal hunting, and natural causes following equations provided by Heisey and Fuller (1985). I bootstrapped the original records 5,000 times using PopTools to not only produce 95% confidence limits for the parameter estimate but also to be entered into the life table 5,000 times to contribute to the estimate of population rate of change (λ). I followed this procedure for adult, subadult, and yearling bears. Some yearlings were collared, but most were monitored as they traveled with their collared mothers. When observers found uncollared yearlings with their mother through the breeding season but did not find them with her later in the summer or fall, then I assumed they were dead. This assumption may lead to a low bias for yearling survival because some did separate from their mothers (but all during the breeding season) and survived. I captured and radio-collared 7 yearlings that had separated from their mothers (mothers of 3 of these had been killed) and included them in the sample.

The annual survival rate for cubs was simply the proportion of those recorded when first seen with their radio-collared mother that was known to be alive the following spring (i.e., just after their first birthday). Each cub within a litter is not independent because, among other reasons, if 1 cub dies, the entire litter is often lost (Swenson et al. 2001a, Mace et al. 2012). Because the estimated variance would be too small if I used each cub as the sample unit (Schwartz et al. 2006), I resampled entire litters (number when first seen and number just after first birthday) with replacement 5,000 times. I used only cubs of mothers that were collared over the entire period. Cubs that died before first observation (i.e., in the maternal den or shortly after emergence) would not be included and thus my estimate of cub survival may be biased high. This bias, however, would be accounted for when estimating λ because the corresponding estimate of reproductive rate would be equally biased low (McLellan 1989a). In some cases, cubs were seen alive in the autumn but were not with their mother when seen the following spring when they would have been yearlings. These cubs possibly survived and separated from their mother as yearlings. When this event happened, I calculated cub survival (and λ) twice; once assuming they lived and again assuming they died.

To estimate age-specific reproductive rates, I tallied females of each age monitored and the number of cubs each produced while at that age. I included individuals monitored for more than 1 year within an age class more than once. For example, a female that was monitored while 5, 6, 7, and 8 years of age and had a litter of 2 cubs when she was 7 would have 0 cubs when 5, and 0, 2, 0 when in the 6, 7, and 8 age class, respectively. This method uses the proportion of females of each age class that produce cubs as suggested by Garshelis et al. (1998), and uses age-class-specific litter sizes in the life table used for population projection with an assumed 50:50 sex ratio of cubs. Because of declining sample size with age, I categorized ages into classes: 5-year-olds (the youngest that a study bear produced a litter), 6–8, 9–12, 13–17, and >17 years. For comparisons among time periods and other study areas, I used the method of Garshelis et al. (1998) to estimate the mean age of primiparity and also interbirth intervals because only using completed intervals is usually biased. Because I did not use intervals to estimate trend but only to compare among time periods, I excluded a 1 year interval when a mother lost her cubs near the time of den emergence and then successfully mated. I estimated reproductive state transition probabilities and stable states following Schwartz and White (2008) for comparison among time periods and other studies.

I estimated population trend by bootstrapping (5,000 times) records of females for 9 vital rates: survival of cubs (using litters as the sampling unit), yearlings, subadults, and adults plus reproductive rates of 5 age classes in PopTools. Because sample sizes were too small to estimate vital rates and population rate of change annually and the land-use treatments and changes in berry production occurred over longer periods of time, I used approximately decade-long intervals or 1979–1988, 1989–1998, and 1999–2010. I used randomization tests (bootstrapping) in PopTools to compare vital rates among decades.

Effect of Age, Bear Density, and Huckleberries on Reproduction and Cub Survival

Female grizzly bears typically produce 0, 1, 2, or 3 cubs the year after breeding. I used logistic regression to estimate the influence of female age, the huckleberry production the summer before cubs were born, and the minimum density of adult female grizzly bears on the probability that a parous

females would produce either small (0 or 1 cub) or large (2 or 3 cub) litters. I excluded nulliparous females and females >22 years of age to avoid confounding influences of reproductive senescence and life-long factors that likely influence age of primiparity.

I also used logistic regression to estimate if cub survival was influenced by the previous year's huckleberry production, adult female density, the size of the litter, if it was a female's first litter, and the number of adult males that were known to have died near the female's home range center because there is evidence of sexually selected infanticide caused by the death of adult males in Scandinavia (Swenson et al. 1997, 2001a). I used each litter as the sample and if any cub was lost, I coded it as 0; if all cubs survived the event, I coded it as 1. I completed the analysis twice; first I assumed that litters seen alive in the autumn but not seen with the radio-collared mother the following year as yearlings had lived and then I assumed that they had died.

Most adult males were killed during the spring hunting season, and therefore I used the number of males that died (most were not radio-collared) over the current and previous year (Swenson et al. 1997, Zedrosser 2009). To account for the likely declining influence of the male with increasing distance from the range of the mother bear, I weighted each dead male by the area of overlap of 2 circles representing average home range size of male (14.6-km radius) and female (8.95-km radius) bears (McLellan and Hovey 2001b) at the distance between where the male died and the arithmetic range center of the mother bear. Males that died within 5.65 km (i.e., $14.6 - 8.95$ km) from the female's home range center would have entirely covered her range so counted as 1 bear. Males killed farther away would have counted only as the proportion of an average female home range that the dead male's range would have overlapped. Adult males killed >23.55 km (i.e., $14.6 + 8.95$ km) from a female's range center would not be counted.

I determined the known minimum density of adult females in the core capture area under the assumption that every adult female that entered this area was eventually captured, radio-collared, and included in the sample. Although I actively avoided recapturing bears until their collars were due to drop off or batteries fail, this assumption was tested by comparing ages of first captures to recaptures in the core capture area. I used only adult females because after 1992 I stopped radio-collaring all males. I used the proportion of radio locations obtained from aircraft or global positioning system (GPS) locations collected over the entire time a bear was monitored that were within the 202-km^2 core capture area as the measure of bear equivalents (Garshelis 1992) or each bear's contribution to density estimate. I included bears in the estimate from when they turned 5 years of age to when they were last known to be alive. I included time between when bears shed radio collars to when they were recaptured in the density estimate. I back-counted adult females caught early in the study for years before they were captured provided they would have been ≥5 years of age. If bears were never recaptured, I assumed they were dead and censored them at the time of collar drop. I continued with capture and

monitoring females for an additional 4 years (to 2014) to help ensure individuals were no longer present. I tallied the sum of all female bear equivalences annually.

In both analyses, I used a mixed effects logistic regression with the individual mother as a random effect. I used Akaike's Information Criterion corrected for small samples (AIC$_c$) to select models most supported by the data and then model averaging to estimate the relative importance of each independent variable (Burnham and Anderson 2002). Because I assumed, a priori, that the causal factors would be independent of each other and each could influence reproductive or survival rates, I first used all possible models as candidates followed by summing Akaike variable weights across all models to estimate the relative importance of each (Burnham and Anderson 2002:167–169, Arnold 2010). I used the glmer package in R (R Development Core Team 2010) followed by the MuMin package for model averaging and estimating relative variable importance.

Comparing an Index of Bear Density Between the Developed and Control Areas

In 2004, Kendall et al. (2009) estimated the population size of grizzly bears in the Northern Continental Divide Ecosystem of Montana using barbed wire hair traps following the method of Woods et al. (1999). The hair traps were moved within a 7×7-km systematic grid approximately every 14 days for 4 sessions. In 2007, Boulanger et al. (2009) used the same method with the same baits across a 6,125-km^2 area in southeastern BC and southwestern Alberta. I did not influence the location of hair traps in either project. Romain-Bondi et al. (2004) demonstrated the strong relationship ($R^2 = 0.88$–0.96) between bear density and the number detected at hair traps even when studies had different cell sizes, used different baits, and were located in ecologically diverse areas. Additionally, the number of bears recorded at hair traps have been used to assess landscape conditions used by grizzly bears (Apps et al. 2004, Graves et al. 2011). I used the number of different grizzly bears recorded at each hair trap as an index of population density. To enable comparisons related to industry, hunting, and huckleberry production, I used the 2 sample randomization test in PopTools to make 2 specific a priori comparisons (Fig. 1): 1) the BC pine flats that had intensive industrial development, grizzly bear and ungulate hunting, and major huckleberry fields to the adjacent Glacier National Park pine flats where there was no industry or hunting but no major huckleberry fields, and 2) the BC Mountains East from the Continental Divide to the pine flats where there was less intensive industrial development but grizzly bear and ungulate hunting, and some smaller huckleberry fields, to the adjacent Glacier Park Mountains that was protected wilderness with no roads.

RESULTS

During the study, I radio-collared 136 different grizzly bears (62 F, 74 M) on 289 occasions and monitored females and males for 226.9 and 79.4 bear-years, respectively. Reproductive rates were based on histories of 45 adult females (Table 1).

Table 1. The number of adult and subadult female grizzly bears, yearlings, and litters of cubs monitored each decade in the Flathead Drainage, 1979–2010. Bear years tracked or number of cubs is in parenthesis. Also included is the number of females in each age category used to estimate reproductive rates. Note the number of cub litters and cubs is less here than in Table 5 because these needed to be tracked until 1 year of age.

Vital rate	1979–1988	1989–1998	1999–2010
Survival			
adult female	16 (39.3)	27 (77.2)	24 (59.1)
subadult female	15 (19.3)	14 (19.7)	10 (12.3)
yearling	27 (15.4)	32 (12.2)	18 (9.5)
cub litters	15 (37)	20 (37)	13 (26)
Reproduction			
5 yr old	9	8	5
6–8 yr old	12	25	10
9–12 yr old	8	26	19
13–17 yr old	11	15	25
>17 yr old	11	11	21

Huckleberry Production

The wet mass of berries in 6, 1-m^2 plots and the mass picked within a 450-m^2 area in 30 minutes were highly correlated to the index of huckleberry production (Spearman $r_s = 0.903$ and 0.964, respectively, $n = 31$, $P < 0.001$). Huckleberry production varied greatly among years in the study area (Fig. 2). In the first decade (1979–1988), the average index was 3.5 (SE = 0.43), in the second (1989–1998) 3.0 (SE = 0.50), but in the third, it was only 1.6 (SE = 0.19), and in 6 of the 12 years the crop failed.

Adult Female Grizzly Bear Density in Core Capture Area

Over the duration of study, I captured and radio-collared 34 different female grizzly bears a total of 117 times in the core capture area. Ten were first captured in the first 4 years of study (1979–1982) and averaged 7.5 years of age (range 0–18). In the next 31 years (1983–2014), 24 additional females were captured in the core area and their average age when first caught was 2.5 years (range 0–7), whereas the average age of the 77 females recaptured was 8.5 years (range 1–31).
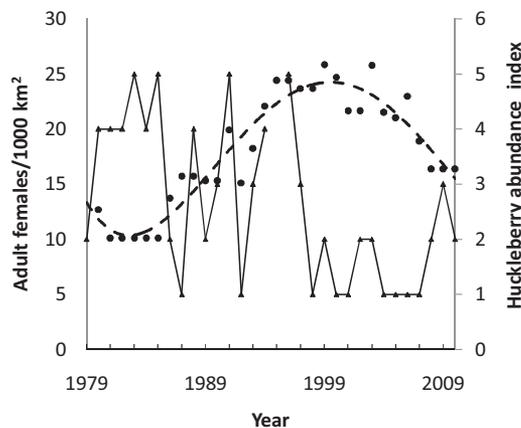
Figure 2. An index of huckleberry abundance (solid line, triangle markers) and minimum density of adult female grizzly bears (bears/1,000 km^2; dotted line, round markers) living in the core capture area between 1979 and 2010 in the Flathead Drainage. The dotted line is a third-order polynomial used only for illustrative purpose.

Of the 101 captures of female bears since 1983, none were >7 years of age when first caught suggesting all females were caught and radio-collared within a few years of leaving their mothers or immigrating into the core capture area. Although at least 1 unmarked adult female entered this area and was not captured (she was killed 2 km inside the area in 1989), 24 radio-collared adult females known to reside at least partially within this area contributed to the minimum density estimates. I counted individual adult females as residents from 1 to 26 years ($\bar{x} = 9.3$ yr) with 5–10 adult females contributing to the density estimate each year. The minimum density of adult females averaged 12.0/1,000 km^2 in the first decade but increased through the second decade when it averaged 20.2/1,000 km^2 and peaked at 25.8/1,000 km^2 in 1999. The minimum density of adult females averaged 21.8/1,000 km^2 in the third decade as it declined to 16.4/1,000 km^2 in 2010 (Fig. 2). When I included dependent offspring and subadult females, the minimum density varied from 16.1 to 55.6 ($\bar{x} = 41.1$) bears/1,000 km^2 excluding independent males.

Causes of Grizzly Bear Mortality

Thirty-two grizzly bears were known ($n = 28$) or suspected ($n = 4$) to have died when carrying functioning radio collars (Table 2). Of these, 1 subadult male was killed by another bear when not fully recovered from immobilization and was considered a research mortality and excluded from other analyses. Five bears (16%) died of natural causes: 1 adult female died in a collapsed den, 2 adult females and 1 subadult male were killed by another bear, and the cause of death of 1 adult female could not be determined. Thus, of the 31 non-research related mortalities, 26 (94% of 16 male deaths and 73% of 15 female deaths) were directly due to people. In the Canadian portion of the study area where grizzly bear hunting was legal, 7 of 13 (54%) male and 4 of 9 (44%) female deaths caused by people were due to legal hunting.

Table 2. Number of known and suspected (in parenthesis) mortalities of radio-collared male and female grizzly bears (including 1 independent yearling) from various causes in the Flathead Drainage by decade, 1979–2010, including the bear that died because of my research.

	Decade						
	1979–1988		1989–1998		1999–2010		
Cause of death	M	F	M	F	M	F	Total
Natural		1	1	2		1	5
Human caused-legal							
Hunter kill	2		4		1	4	11
Research	1						1
Accident					1		1
DLP[a]						3	3
Human caused-illegal							
DLP[a]	(1)		1 (3)				1 (4)
Hunter kill		1					1
Malicious		1					1
Poach		2					2
Unknown			1		1		2
Total human caused	3 (1)	4	6 (3)	0	3	7	23 (4)
Total	3 (1)	5	7 (3)	2	3	8	28 (4)

[a] Defense of life or property.

Table 3. Dates and duration of the 6 intervals used to estimate annual survival rates of radio-collared grizzly bears in the Flathead Drainage, 1979–2010, excluding the bear that died because of research and the 1 collared yearling. The number of bears known plus suspected to have died, total bear-months of monitoring, and the monthly mortality rates for each interval are presented for male and female radio-collared bears.

| | | Interval | | | | | |
	Sex	Pre-berry little hunting	Pre-berry heavy hunting	Pre-berry no hunting	Berry no hunting	Post-berry ungulate hunting	Winter no hunting
Dates		15 Apr–10 May	11 May–5 Jun	6 Jun–31 Jul	1 Aug–20 Sep	21 Sep–30 Nov	1 Dec–14 Apr
Duration (days)		26	26	56	51	71	135
Dead bears	F	0	6	1	0	6	1
	M	0	9	2	0	4	1
Months[a] tracked	F	191	188	431	396	546	1,010
	M	70	64	152	129	187	352
Monthly[a] mortality rate	F	0	0.032	0.002	0	0.011	0.001
	M	0	0.141	0.013	0	0.021	0.003

[a] Using a 30-day month.

Survival Rates

Daily mortality risk varied greatly among the 6 intervals (Table 3). Risk during pre-berry with heavy grizzly hunting was about 3 and 7 times higher for female ($P = 0.018$) and male ($P < 0.001$) bears, respectively, than during post-berry with ungulate hunting, which was the second most risky interval. The risk of death during the other 4 intervals was much lower; only 17% of the deaths occurred during these intervals although they accounted for 74% of the time bears were monitored ($P < 0.001$; Table 3).

The survival rate of adult males pooled over the entire study was 0.84 (95% CI = 0.73–0.93) when 6 known and 1 suspected mortality were included but 0.86 (0.76–0.95) when the suspected mortality was excluded. For subadult males,

the survival rate was 0.78 (0.67–0.89) but 0.85 (0.75–0.95) when 3 suspected mortalities were excluded. Even when I excluded suspected mortalities, adult males had a lower survival rate than 0.93 (0.89–0.97) of adult females ($P = 0.029$), and subadult males had lower survival than 0.96 (0.89–1.00) of subadult females ($P = 0.031$). The mortality rate due to legal hunting of subadult and adult females pooled was 1.8%, for all other human-caused deaths it was 2.5%, and for natural causes it was 1.7%. For subadult and adult males pooled, these rates were 9.0%, 8.9%, and 1.1%, respectively, when suspected kills were included. Subadult female survival remained similar over the 3 decades (Table 4), whereas adult female survival appeared to decline in the third decade ($P = 0.062$). When sample size was increased by pooling adult and subadult females, the decline in female survival in decade 3 was more apparent ($P = 0.045$).

Over the entire study, yearling survival was 0.86 (0.74–0.96) and cub survival was 0.70 (0.57–0.83) if cubs seen alive in the autumn but were not with their mother the following year had died but 0.81 (0.70–0.91) if they lived (Table 4). I

Table 4. Vital rates and population trend of female grizzly bears and cubs and yearlings of both sexes during each decade period and all 3 decades pooled in the Flathead River Drainage, 1979 to 2010 with 95% confidence limits in parenthesis.

Vital rate	1979–1988	1989–1998	1999–2010	1979–2010
Survival				
Ad (S_{5+})	0.93 (0.83–1.00)	0.97 (0.93–1.00)	0.89 (0.80–0.96)	0.93 (0.89–0.97)
SubAd (S_{2-4})	0.93 (0.79–1.00)	1.00 (1.00–1.00)	0.94 (0.74–1.00)	0.96 (0.89–1.00)
Yearling (S_1)	0.86 (0.66–1.00)	0.78 (0.56–0.96)	1.00 (1.00–1.00)	0.86 (0.74–0.96)
Cub (S_0)[a]	0.84 (0.64–1.00)	0.86 (0.70–1.00)	0.69 (0.42–0.92)	0.81 (0.70–0.91)
Cub (S_0)[b]		0.70 (0.50–0.88)	0.50 (0.23–0.77)	0.70 (0.57–0.83)
Reproduction				
5 yr old (m_5)	0.22 (0–0.56)	0.06 (0–0.19)	0.10 (0–0.30)	0.14 (0.02–0.27)
6–8 yr old (m_{6-8})	0.25 (0–0.50)	0.20 (0.06–0.36)	0.15 (0–0.35)	0.20 (0.10–0.32)
9–12 yr old (m_{9-12})	0.50 (0.13–0.88)	0.29 (0.12–0.48)	0.21 (0.05–0.42)	0.29 (0.17–0.42)
13–17 yr old (m_{13-17})	0.50 (0.14–0.91)	0.30 (0.1–0.5)	0.20 (0.04–0.40)	0.30 (0.16–0.44)
>17 yr old (m_{17+})	0.41 (0–0.82)	0.36 (0–0.73)	0.22 (0.05–0.40)	0.30 (0.15–0.47)
Trend				
λ[a]	1.074 (0.985–1.151)	1.080 (1.027–1.125)	0.980 (0.892–1.058)	1.046 (1.001–1.085)
λ[b]		1.061 (1.001–1.106)	0.955 (0.868–1.032)	1.033 (0.990–1.072)

[a] Rates assuming cubs seen in the fall but not the following spring survived.
[b] Rates assuming cubs seen in the fall but not the following spring died.

assumed 6 cubs in 3 litters to have died because their mother was shot. If these human-caused mortalities are excluded, then cub survival was 0.74 (0.61–0.86) if cubs seen alive in the fall died or 0.86 (0.76–0.95) if they survived. Cub survival was lower in the third decade than the first 2 combined if cubs seen in the autumn but not seen with the mother the following spring had died ($P = 0.040$). If these cubs lived, cub survival in the third decade would not be as distinctly lower than the first 2 decades combined ($P = 0.091$). When the cubs from the mothers that were shot are excluded, then cub survival in the third decade was similar to the previous 2 decades if cubs seen in the fall but not the following spring survived ($P = 0.634$) or died ($P = 0.217$).

Reproductive Rates

The reproductive rate averaged 0.257 (95% CI = 0.198–0.320) female cubs/yr/female ≥ 5 years old over the study period but varied over the decades (Table 4). During the first decade, the reproductive rate was 0.374 (95% CI = 0.225–0.539) and this declined to 0.254 (95% CI = 0.165–0.353) in the second decade ($P = 0.072$). By the third decade, the reproductive rate was only 0.192 (95% CI = 0.105–0.290) and unlikely to be the same as the pooled results of the previous 2 decades ($P = 0.045$). Because of high reproduction in the first decade but a decline through the second, the third decade had a higher proportion of older females that were born in the first decade and first portion of the second decade and fewer young females.

The average age of primiparity was 6.60 (95% CI = 5.67–6.67) and 7.09 (95% CI = 6.20–8.33) during the first 2 decades but increased ($P = 0.001$) to 10.46 (95% CI = 8.56–12.00) years in the third decade (Table 5). During the third decade, 9 females ≥ 5 years of age were monitored before having cubs, but only 4 of these had their first litter while being monitored. Of these, 2 were 5 and 6 years of age and 2 others were 12 years old. Additionally, 2 females were monitored from when they were 5 to 7 years of age and a third was tracked from 5 to 9 but they did not have their first litter at these ages.

Interbirth intervals (yr/litter) appeared to increase from 2.93 years in decade 1 to 3.44 years in decade 2 ($P = 0.144$), and then to 4.22 years in decade 3 ($P = 0.083$; Table 5).

Although these decade to decade differences were not clearly different, it was highly unlikely ($P = 0.006$) that intervals in decade 1 were the same as in decade 3 or intervals during decades 1 and 2 pooled were the same ($P = 0.019$) as during decade 3. The average litter size declined after the first decade ($P < 0.001$; Table 5).

Using all data (1979–2010), a regression weighted by sample size suggested that average litter size increased with the age of the mother ($R^2 = 0.426$, $\beta = 0.065$, $P = 0.003$) and litters of primiparous females were smaller ($\bar{x} = 1.54$, $n = 13$) than subsequent litters ($\bar{x} = 2.12$, $n = 41$; $P = 0.003$). Similarly, the average number of cubs produced per female per year increased with age when all adult females, including those that had not yet had cubs, were included in a regression weighted by sample size ($R^2 = 0.371$, $\beta = 0.080$, $P = 0.007$), but the relationship was not linear across their life (Fig. 3). The reproductive rate was low for young females (<8 yr), higher for prime-aged females, and declined later in life suggesting senescence. Only 8 females ≥ 20 years of age were monitored, which was an insufficient number to compare senescence among decades. There was no indication that 5 of these older females had reproductive senescence when they died or shed their collars, but the oldest bear to have a litter was 22 years. The 3 other bears did not have cubs when they could have (i.e., were not with cubs, yearlings, or 2-year-olds) for 2, 3, and 4 consecutive years suggesting a reduction in reproduction. Only 2 bears were tracked for their entire reproductive lives and 1 gave birth to 8 and the other 17 cubs. A third female produced 11 cubs, but she may have had 1 other litter because I missed monitoring her for 2 of her 21 years of life.

I recorded 182 reproductive state transitions from 43 female grizzly bears that transitioned from 4 to 5 years of age or between older ages. Of these, 28 (65%) were first captured when nulliparous, 3 were alone, 4 were with cubs, 6 were with yearlings, and 2 were with 2-year-olds. Transition probabilities and therefore stable states differed among decades (Table 6). Notably, data from the first decade reflected consistent, usually 3-year interbirth intervals. Only 12 of 45 (27%) transitions were from alone to alone and only 1 of these was of a parous female (2% of transitions); the others had not yet had their first litter. In the second decade,

Table 5. Reproductive parameters of female grizzly bears during 3 decades in the Flathead River Drainage, 1979 to 2010 and all decades pooled.
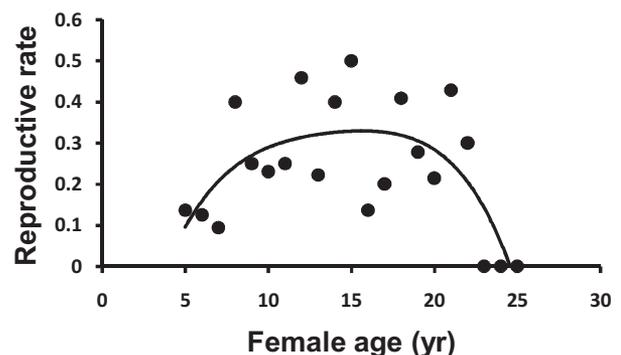
Parameter	1979–1988	1989–1998	1999–2010	1979–2010
Average age of primiparity (yr)[a] ($n \geq 5$ yr monitored, n had first litters)	6.60 (10, 6)	7.09 (8, 5)	10.46 (9, 4)	8.19 (27, 15)
Inter-birth interval (yr)[a] (all intervals, completed intervals)	2.93 (12, 11)	3.44 (15, 11)	4.22 (11, 6)	3.55 (38, 28)
Litter size (n litters) (CI)	2.37 (16) (2.13–2.63)	1.79 (24) (1.54–2.04)	1.82 (17) (1.47–2.18)	1.96 (57) (1.77–2.14)

[a] When females were monitored across 2 decade periods for this parameter, their information was placed in the period with most monitoring.

Figure 3. The reproductive rate (female cubs/female/yr) of female grizzly bears monitored (including females with no cubs) between 5 and 25 years of age in the Flathead Drainage, 1979 to 2010. The line is a fourth-order polynomial used only for illustrative purpose.

Table 6. Stable reproductive states of female grizzly bears (≥4 years old) during each of 3 decades and all years together based on reproductive state transition probabilities in the Flathead River Drainage, 1979 to 2010.

Status	1979–1988	1989–1998	1999–2010	1979–2010
Alone	0.107	0.435	0.555	0.412
Cubs	0.346	0.249	0.201	0.252
Yearlings	0.283	0.171	0.124	0.177
Two-yr-olds	0.226	0.145	0.103	0.146
Three-yr-olds	0.040	0.000	0.017	0.012

22 of 71 (31%) transitions were alone to alone and 4 of these were parous females (6% of transitions). In the third decade, 28 out of 66 (42%) transitions were alone to alone and 13 of these were of parous females (20% of transitions), suggesting mature females were missing more birthing opportunities ($G_2 = 8.58$, $P = 0.014$). Multiplying average litter size by the stable state of being with cubs suggested reproductive rates were 0.410, 0.223, and 0.183 for decades 1, 2, and 3, respectively.

Rate of Change
The best estimate of the survival–fecundity rate of increase (λ) was 1.074 for the first decade and 1.061 to 1.080 (depending on cub survival) for the second, suggesting an increasing population assuming a stable age distribution and no immigration or emigration (Table 4). In the third decade (1999–2010), the estimate of λ declined to between 0.955 and 0.980.

Factors Influencing Reproduction of Individuals
The mixed effects logistic regression suggested the model with most support to predict if a parous female would have a small or large litter included the previous year's huckleberry production and the density of adult females (Fig. 4). Other competitive models included only previous year's huckleberries ($\Delta AIC_c = 1.05$), the full model ($\Delta AIC_c = 1.38$), and only adult female density ($\Delta AIC_c = 1.40$). Averaged variable weights suggested that the previous year's huckleberry abundance followed by density were the most important predictor variables influencing the production of large or small litters (Table 7).

The full model explained 30% of the variation in whether or not a parous female would produce a small or large litter suggesting other factors also influence annual cub production. I recorded cub production on 2–6 occasions for 18 parous females. Four females never had a litter of >1 cub in 14 opportunities although on 2 occasions, the birth followed years with class 4 huckleberry abundance. Four other females always had litters of ≥2 cubs in 14 opportunities. Although these 4 mothers lived when huckleberry production was higher, 1 female produced ≥2 cubs in all of 6 opportunities including a 3 cub litter following a year with almost no huckleberries. Three other females had 3 cub litters following years with almost no berries.

Factors Influencing the Survival of Cub Litters
Of 48 litters seen in the spring, all cubs in 37 litters survived at least to the autumn; no cubs survived in 9 litters (3 litters because the mother was shot), and 2 litters had partial cub loss. No cubs in 6 of the litters seen in the autumn were with
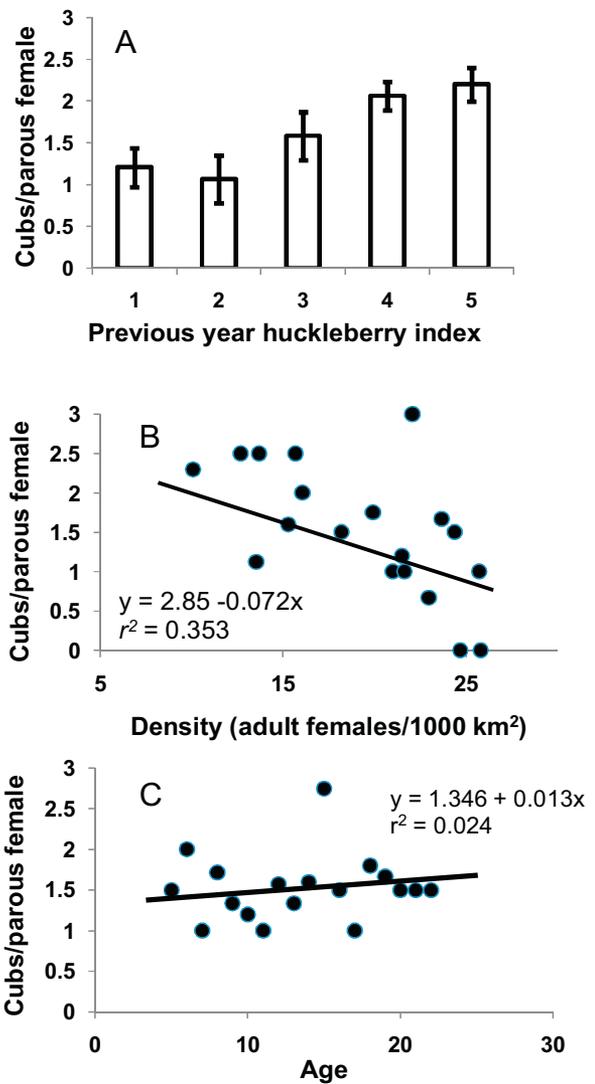
Figure 4. The average number of grizzly bear cubs produced per parous female that was alone and available to breed the previous year and (A) the huckleberry production index the previous year with standard error bars, (B) adult female density in the core trapping area with the line weighted by sample size, and (C) age of the adult female with the line weighted by sample size. I excluded females >22 years of age because I assumed they were in reproductive scenence. Data are from the the Flathead Drainage, 1979 to 2010.

Table 7. Relative importance of female age, adult female density, and previous years' huckleberry crop (berries) for predicting whether or not a parous grizzly bear female would have a small (0 or 1) or a large (2 or 3) litter of cubs when she was alone and available to have bred the previous breeding season in the Flathead Drainage, 1979 to 2010. Analysis is based on a mixed effects logistic regression, with female ($n = 29$) specified as the random intercept ($n = 72$ litters; some had 0 cubs) and I show the coefficients with standard errors and relative importance (AIC wt) of factors. The adjusted R^2 for the complete model was 0.30.

Variable	Coefficient (SE)	Standardized coefficient (SE)	AIC wt	P
Intercept	1.01 (2.28)			
Berries	0.56 (0.26)	1.50 (0.71)	0.76	0.033
Density	−0.15 (0.07)	−1.54 (0.77)	0.71	0.044
Age	0.06 (0.07)	0.55 (0.65)	0.31	0.396

the mother when she was seen the following year so they may have perished or separated from the mother as yearlings. When litters seen in the fall but not seen the following year were assumed to have lived, the model with most support to predicting cub loss included only if the mother was primiparous (Table 8). The intercept-only model was the next best ($\Delta AIC_c = 0.43$) suggesting the other factors had little effect and variable weights suggest that primiparity was the only factor that may have had some, albeit weak, influence on cub survival. When the 6 litters seen in the autumn but were not seen with their mother the following year were assumed to have died, then the best supported model included adult female density and if the mother was primiparous (Table 9); all others had $\Delta AIC_c > 2.0$. Litter size, huckleberry crop the previous year, and the number of adult males killed near the mother's range center in the previous 2 years ($\bar{x} = 1.94$, range 0–6 killed within 23.55 km) had no discernable influence on cub survival.

Spatial Comparisons of Grizzly Bear Density Indices

The BC Pine Flats had an average of 0.84 bears/hair trap site (0.63 F, 0.21 M) recorded, which is almost 4 times the average of 0.23 bears/site (0.16 F, 0.07 M) recorded in 31 sites in Glacier Park Pine Flats ($P = 0.008$; Fig. 5). The BC Mountains East between the Continental Divide and the Pine Flats had an average of 0.62 bears/site (0.28 F, 0.34 M) over 32 sites, which may not have been different ($P = 0.149$) from the 0.44 bears/site (0.11 F, 0.33 M; Fig. 5) recorded at 36 sites in the respective mountainous portion of Glacier National Park. There were 2.5 times more females detected per site in BC than in the United States ($P = 0.002$) but only 1.4 times as many males ($P = 0.120$).

DISCUSSION

Over the past century, protected areas were critical for the conservation of grizzly bears in the contiguous United States. Most grizzly bears in North America, however, live outside of protected areas in Canada and Alaska where there is continued human expansion across the landscape, primarily

Table 8. The relative importance of litter size, the number of adult males killed in previous 2 years weighted by area overlap with mother (dead males), adult female density (density), previous years huckleberry crop (berries), and whether or not the litter was the female's first (primiparity) for predicting whether or not a grizzly bear female would lose at least 1 cub in the Flathead Drainage, 1979 to 2010. Cubs seen in the autumn but not seen with the mother the next spring are assumed to have lived. Litters lost because the mother was shot are excluded. Analysis is based on a mixed effects logistic regression, with female ($n = 20$) specified as the random intercept ($n = 43$ litters) and I show the coefficients with standard errors and relative importance (AIC wt) of the factors. The adjusted R^2 for the complete model was 0.15.

Variable	Coefficient (SE)	Standardized coefficient (SE)	AIC wt	P
Intercept	1.97 (1.58)			
Primiparity	−1.54 (0.92)	−1.63 (0.97)	0.53	0.094
Density	−0.06 (0.08)	−0.88 (1.20)	0.28	0.461
Dead males	0.33 (0.63)	0.70 (1.37)	0.25	0.610
Berries	0.14 (0.36)	0.48 (1.25)	0.24	0.700
Litter size	0.12 (0.67)	0.23 (1.24)	0.23	0.852

Table 9. The relative importance of litter size, the number of adult males killed in previous 2 years weighted by area overlap with mother (dead males), adult female density (density), previous years huckleberry crop (berries), and whether or not the litter was the female's first (primiparity) for predicting whether or not a grizzly bear female would lose at least 1 cub in the Flathead Drainage, 1979 to 2010. Cubs seen in the autumn but not seen with the mother the next spring are assumed to have died. Litters lost because the mother was shot are excluded. Analysis is based on a mixed effects logistic regression, with female ($n = 20$) specified as the random intercept ($n = 43$ litters) and I show the coefficients with standard errors and relative importance (AIC wt). The adjusted R^2 for the complete model was 0.42.

Variable	Coefficient (SE)	Standardized coefficient (SE)	AIC wt	P
Intercept	5.46 (2.47)			
Density	−0.23 (0.09)	−2.72 (1.06)	0.97	0.010
Primiparity	−2.28 (1.03)	−1.94 (0.87)	0.83	0.026
Berries	0.27 (0.39)	0.75 (1.10)	0.26	0.495
Dead males	−0.20 (0.53)	−0.35 (0.92)	0.23	0.700
Litter size	0.20 (0.63)	0.30 (0.94)	0.23	0.748

to develop natural resources. Even in the lower 48 states, grizzly bears are expanding out of protected areas (Schwartz et al. 2006, Kendall et al. 2009, Mace et al. 2012) and future gains in numbers and distribution will largely be on multiple use lands. For effective conservation of the species, it is important to understand how top-down and bottom-up factors influence grizzly bears both inside and out of protected areas.
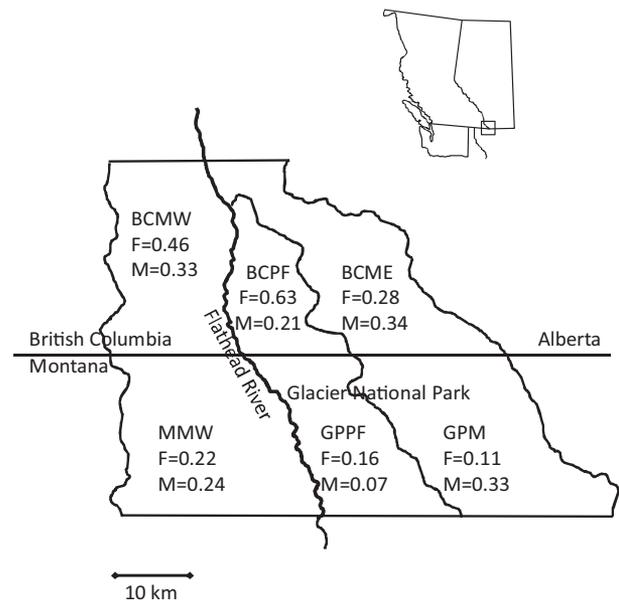
Figure 5. The average number of male and female grizzly bear detections at each hair trap in the British Columbia (BC) Mountains West (BCMW), BC Mountains East (BCME), Montana Mountains West (MMW), and the Glacier Park Mountains East (GPME). The main comparison for this study was between the BC Pine Flats (BCPF), where there had been intensive industrial development and grizzly bear hunting but also major huckleberry fields, with the Glacier Park Pine Flats (GPPF) that had no industrial development or hunting but also no major huckleberry fields. Data were collected in 2004 in the United States and 2007 in BC.

Industry and Human-Caused Mortality

Across at least the southern portion of their distribution in North America, >80% of grizzly bears older than yearlings are eventually killed by humans and most mortalities are near a road, camp, or permanent settlement (McLellan 1989*b*, 1999; Garshelis et al. 2005; Schwartz et al. 2006, 2010; Boulanger and Stenhouse 2014). No collared bears in my study were killed at industrial camps, but these industries developed new roads from which bears were killed, indirectly linking industry to bear mortality (McLellan 1989*a,b*; Ciarniello et al. 2009; Schwartz et al. 2010; Boulanger and Stenhouse 2014).

Of the bears that died in my study, most were killed by land owners at their residences, legal grizzly bear hunters, or ungulate hunters. Converting public to private land is a policy issue unrelated to recent industrial roads in my study area. Because of the annual draw for a limited number of permits, the number of grizzly bear hunters depends on previous hunter success. Increasing hunter efficiency on an expanded road network does not necessarily increase the number of bears killed because permit numbers decline when success increases. Ungulate hunters killed bears that were attracted to their camps or when they felt threatened by the bear. Because ungulate hunters are not searching for grizzly bears, the number of encounters between bears and these hunters depends mostly on the number of hunters in grizzly bear habitat. Once the road network enables ungulate hunters to easily enter the home range of a bear, then further increases in road density may disperse hunters but will not necessarily increase encounter rates unless the overall number of hunters increases. Although bears were most often shot near roads, the increase in road density likely did little to increase the number of bears shot by ungulate hunters. The number of hunters in the study area actually declined over the study period (BC Ministry of Forests, Lands and Natural Resource Operations Hunter Survey Database, Victoria, BC).

New industrial roads likely contribute to the number of bears poached. Increased road density would enhance the efficiency of poachers searching for bears just as it enhances the efficiency of legal hunters but, of course, legal limits do not affect poachers. Only 2 of the 26 known or suspected human caused deaths were due to poaching suggesting it was not common in my study area. It is possible that in some circumstances, wearing a radio collar influenced whether or not a bear was shot, but almost all collars I deployed (210 of 231) were small brown or black VHF collars and not easily seen.

Industry and Bottom-Up Processes

The industry and other human activities affected the distribution and behavior of grizzly bears in my study area (McLellan and Shackleton 1988, 1989*a,b*) and in other areas (Kasworm and Manley 1990, Mace et al. 1996, Ciarniello et al. 2007). Nevertheless, the industrial activities did not have a clear negative effect on population trend as predicted. Not only was λ positive during the decade with industrial development and the decade following, but more bears per hair trap were detected in the industrialized pine flats north of the border than similar areas in the protected control area. Thus, contrary to expectation, these industrial activities may appear to have benefited bears, however, because grizzly bears rarely used logged areas (McLellan and Hovey 2001*a*), a causal link is unlikely.

The increasing trend of the grizzly bear population was more likely due to the change in people's attitudes towards carnivores from the mid-1950s through the 1970s that ended decades of excessive killing. In the mid 1950s, predator control declined along the western boundary of Glacier National Park (Keating 1986) and in BC, the widespread use of poison to control predators (primarily wolves) was stopped in 1961 (Archibald 1989). The use of bait for hunting grizzly bears in BC was discontinued in 1968, in 1971 the general open season in the fall was closed, and in 1977, a year before my study began, the hunt became tightly controlled by a draw for a limited number of spring-only permits. In 1975, the grizzly bear was listed as a threatened species in the United States, which may have further influenced how biologists, conservation officers, and the public valued grizzly bears. A similar increasing trend in grizzly bear numbers was reported in the Northern Continental Divide (Keating 1986, Mace et al. 2012) and Greater Yellowstone ecosystems (Schwartz et al. 2006).

During the first decade of study that coincided with the industrial activity, the grizzly bear population had high reproductive and juvenile survival rates compared to later decades as well as compared to other areas in the interior of the continent (Wakkinen and Kasworm 2004, Garshelis et al. 2005, Schwartz et al. 2006, Mace et al. 2012). These bears maintained these rates even though they avoided roads and industry during spring and fall (McLellan and Shackleton 1988). Displacement during these seasons may not have affected foraging efficiency because major foods at that time of year (grasses, herbs, roots) were widespread but of low energy content (McLellan and Hovey 1995), and remained abundant throughout the season. During the summer, bears foraged primarily on huckleberries (McLellan and Hovey 1995) in areas that had been burned by wildfire and there they rapidly deposited fat needed for successful hibernation and reproduction (McLellan 2011). There were no roads into any of these burns so bears were rarely disturbed. When bears were disturbed in this habitat by intensive helicopter-supported seismic exploration, there was little displacement (McLellan and Shackleton 1989*a*). The lack of negative impact of industry on bottom-up processes was likely because grizzly bears avoided areas of predictable human activity at lower elevations where foods were abundant but of lower quality; bears likely were rarely disturbed when foraging on high-energy foods growing in higher elevation post-fire habitat.

Ecological Factors Affecting the Grizzly Bear Population

On a continental scale, grizzly bear densities vary by 2 orders of magnitude (McLellan 1994, Miller et al. 1997, Hilderbrand et al. 1999). The variable, omnivorous diet of grizzly bears, combined with the anadromous and semelpa-

rous behavior of salmon that provide bears with an enormous amount of high-quality food in some coastal areas, enables dramatic contrasts in bear density. But even in areas without spawning salmon, food plays a major role in determining grizzly bear population density (McLellan 2011).

For an area without salmon, the Flathead had a high density of grizzly bears (Boulanger et al. 2009). McLellan and Hovey (1995) suggested that the high density was because most major bear foods found across the interior of North America were common. More specifically, McLellan (2011) suggested that the high density was due to the abundance of fruit and particularly huckleberries because this food dominated the bears' diets in August and September when body composition measurements indicated rapid increases in fat reserves. The hypotheses that high-energy summer and fall foods as well as bear density influenced bottom-up population processes were supported in this study.

In the first decade of study, the population density was relatively low, huckleberries were usually abundant, and the population was increasing with one of the highest rates of reproduction and cub survival recorded for this species in North America despite the industrial activity. During the second decade, there was little industry, huckleberry productivity generally remained high, and bear density continued to increase. During this decade, the reproductive rate was beginning to decline because of smaller litters and likely longer interbirth intervals, suggesting a density effect. At the start of the third decade, population density reached its maximum and the average huckleberry production declined and often failed. During this decade, the reproductive rate, which previously had been among the highest recorded in North America, was now among the lowest with small litters, extended interbirth intervals, and an older age of primiparity. Even in an area with an abundance of other foods, the combination of a high density of bears and greatly reduced huckleberry production had dramatic changes on recruitment and the population was in decline.

My analysis of individual reproductive events also suggested that both huckleberry abundance the previous year and female density influenced reproduction. In both my study and in the Yellowstone ecosystem, top models predicting cub production had indices of bear density and the previous year's production of the major energy producing plant food in the ecosystem, huckleberries in the Flathead and whitebark pine (*Pinus albicaulis*) seeds in Yellowstone (Schwartz et al. 2006).

Bears in my study area rapidly deposited fat when foraging on both huckleberries and buffaloberries (*Shepherdia canadensis*; McLellan 2011), but a direct link between maternal body fat and cub production has not clearly been established for wild grizzly bears. Robbins et al. (2012), however, found captive adult females with <20% body fat in the autumn never produced a litter even though they mated the previous spring. In other bear species, Belant et al. (2006) found reproduction of American black bears to be strongly influenced by body fat with twice as many females having litters following a year when they became fat than years when they were thin. Molnár et al. (2011) found fatter polar bears (*U. maritimus*) had larger litters. Several studies of American black bears have found reproductive rates to decline following years when the major energy foods in the system failed (Rogers 1976, Elowe and Dodge 1989, Costello et al. 2003, Obbard and Howe 2008).

The mechanistic link between the decline in a major energy food and reduced reproduction of grizzly bears is supported in my study; however, the previous year huckleberry crop and bear density only explained 30% of the variation in the production of small or large litters. The variation in cub production among individuals was large with some producing large litters even when fruit production was low the previous summer, whereas other females failed to have cubs or produced only single-cub litters when fruit had been abundant. It appears that some individuals were more skilled than others at obtaining sufficient nutrients even under adverse conditions and were consistently more productive. The more pronounced decline in bear reproduction during the decade-long reduction in huckleberries suggests that consecutive years of reduced food may have a greater effect on reproduction than do year-to-year fluctuations.

Eberhardt (1977, 2002) suggested juvenile survival should be the first vital rate to change as populations approach carrying capacity and both Miller et al. (2003) and Schwartz et al. (2006) found density to effect grizzly bear cub survival. My results were less clear, perhaps because only a few litters lost any cubs at least before autumn. Cub survival remained similar through the first and second decades but appeared to decline in the third decade when berries often failed and bear density was initially high. However, when I excluded cub mortalities due to mothers being shot, then cub survival was not significantly reduced. Similarly, none of the a priori factors clearly influenced cub loss unless I assumed all cubs seen alive in the autumn but not the following year had died. Then, bear density and whether the mother was primiparous were related to cub loss. In Yellowstone, Schwartz et al. (2006) found young females lost litters more often than older females and primiparous brown bears in Scandinavia lost litters more often than multiparous females (Zedrosser et al. 2009).

The form of sexually selected infanticide shown by brown bears in Scandinavia, called the "immigrant male hypothesis" (McLellan 2005) predicts cub survival will be reduced when adult male bears are killed by hunters because immigrant males replacing the dead male are prone to kill unrelated cubs (Swenson et al. 1997, 2001*a*). Because grizzly bears are not territorial but have large, overlapping home ranges and a scramble competition mating system (McLellan 2005, Steyaert et al. 2012), a second form, called the "mate recognition hypothesis" (McLellan 2005) predicts increased cub survival when the relative abundance of adult males is decreased, because all males in the area except the father are potentially infanticidal. In my study and in the Yellowstone ecosystem (Schwartz et al. 2006), the number of adult male bears killed near the range of mother bears in the previous 2 years was not in any top models predicting cub survival and had little weight. Similarly, comparisons between American

black bear cub survival in adjacent hunted and unhunted areas found no difference (Obbard and Howe 2008) or higher survival in the hunted area (Czetwertynski et al. 2007), suggesting the immigrant male hypothesis of sexually selected infanticide documented in Scandinavia was not supported.

My study cannot directly evaluate the mate recognition hypothesis of sexually selected infanticide, but results show high cub survival through to the autumn in an area where 67% of the adult bears killed by hunters were males and the adult male harvest density (adult males killed/yr/km^2) was 34 times that of the Scandinavian study were infanticide was reported (Swenson et al. 1997). These results suggest that reducing the relative abundance of adult males, who are known to kill cubs as well as older bears (McLellan 1994; Swenson 2001a,b), may even enhance cub survival (McLellan 2005).

The growth rate of large mammal populations is most sensitive to a change in adult female survival (Knight and Eberhardt 1985, Taylor et al. 1987, McLellan 1989a), but this parameter is thought to be least influenced by density (Eberhardt 1977, 2002; Bonenfant et al. 2009). I found a decline in female survival during the third decade when densities were high and huckleberries more often failed due to a marked increase in the number of females killed by bear and ungulate hunters. Females with attendant offspring are protected from hunting so, with a springtime hunt, few were vulnerable in the first decades when almost all had offspring. In the third decade, adult females were more often alone and vulnerable. Females killed by ungulate hunters were in the valley where hunters camp and usually hunt. In years with abundant huckleberries, these bears would have likely been at higher elevation, unroaded berry fields where hunters rarely go. It is less likely that they would have been killed if the huckleberry crop was similar to what it had been in the previous decades.

The results of my study suggest that both density-dependent and density-independent factors interacted to influence grizzly bear population size. Although causal mechanisms vary among species, locations, and time periods, interactions between density dependent and independent factors appears common (Saether 1997, Portier et al. 1998, Owen-Smith 2006, Bonenfant et al. 2009) and will likely become increasingly apparent with more long-term and detailed studies of ecological conditions and vital rates.

Spatial Comparisons of Grizzly Bear Density Indices

Bears on the BC side of the Canada–United States border likely had reduced detection rates at baited hair-traps because they had been captured using foot snares for 2 decades and were likely wary of bait, human-scent, and wire (Boulanger et al. 2004). Even with possible reduced detectability, almost 4 times as many bears per site were detected in the pine flats north of the border than in the pine flats in Glacier National Park. Because bears rarely used logged areas (McLellan and Hovey 2001a), the logging itself unlikely influenced the apparent difference in bear abundance. Human settlement along the western boundary of Glacier Park has likely resulted in unrecorded human-caused mortality, but the rate, particularly for females with small home ranges that may not reach the park boundary, would unlikely have been sufficient to depress the population to a quarter of that in BC; no female bears monitored by Mace et al. (2012) were killed because of the settlement. The abundance of large huckleberry fields adjacent to the BC Pine Flats compared to the lack of large huckleberry fields adjacent to the Glacier Park Pine Flats was likely the primary factor responsible for the difference in grizzly bear numbers. If areas recently burned by wildfires in Glacier National Park follow the same succession pattern as the 1930s fires did north of the border, then I predict a substantial increase in bear density in the northwestern portion of Glacier Park in decades to come. The fire history north of the border that provided both an abundance of high-energy food and no incentive for road building to access timber likely enabled the grizzly bear population to not only buffer the industrial activity but also thrive during that period. Without the abundance of berries in unroaded basins, results of this study would likely have been different.

When I pooled the number of bears detected per site for all 3 areas north of the border and compared it to the number south of the border, there were 1.4 times as many males but 2.5 times as many females recorded per site north of the border. The difference in sex ratio of bears sampled between the 2 countries was likely due to male-biased hunting north of the border. Removing about twice as many males as females may affect population processes in several ways. Bear density affects reproduction (Schwartz et al. 2006, this study) and removing males would leave more resources for females and their offspring. In addition, adult male grizzly bears are known to kill other bears (McLellan 1994, 2005; Swenson et al. 1997, 2001a,b) and a higher proportion of adult males in a population may displace some females into subprime habitats (Wielgus and Bunnell 1995, Ben-David et al. 2004). In my study area, differences in habitat selection between males and females were not detected (McLellan and Hovey 2001a). In contrast to the potentially positive effects of hunting on bear density, 33% of the bears killed were females and population trend is sensitive to adult female survival (Taylor et al. 1987, McLellan 1989a). Hunting was likely the cause of the different sex ratio between the hunted and unhunted portion of the Flathead valley, but the effect on the unequal density of bears is equivocal.

I focused my study on a relatively small area to match the spatial scale of the industrial development. Given the restricted spatial scale, the dramatic changes in vital rates of Flathead grizzly bears may be unusual when viewed across larger spatial scales. However, fruit production of shrubs partially depends on fire history (Martin 1983, McLellan and Hovey 2001a), which is influenced by climatic conditions, so suitable successional stages for berry production is likely widespread because of droughts across western North America in the 1920s and 1930s (Pederson et al. 2006). Fruit production also depends on weather patterns (Krebs et al. 2009, Holden et al. 2012) that also operate over large spatial scales. The annual estimates of huckleberry produc-

tion 130 km southwest of my study area (Holden et al. 2012) were positively correlated with my estimates (Spearman $r_s = 0.49$, $P = 0.018$) and there production was below average for 9 consecutive years between 1997 and 2005, which is similar to production in my study.

MANAGEMENT IMPLICATIONS

A significant implication of my study is how the abundance of a high-energy food source growing in undisturbed portions of the study area enabled this bear population to increase in spite of intense industrial development and with the highest density of hunter-killed bears in BC. Once this food source declined, the grizzly bear population declined because of reduced reproduction and more females being without cubs and thus being vulnerable to legal hunting. Managers should identify which high-energy foods such as berries, salmon, whitebark pine seeds, or ungulates are important in various ecosystems and try to maintain or enhance these foods while reducing human access into habitats where they are abundant. Although the density of hunter-killed bears was high, I found that people killed as many collared bears for reasons other than legal hunting and the mortality rate of female bears was less for hunting than it was for other causes. Considerable effort has been directed towards reducing conflicts near settlement and agricultural areas, yet in many regions, bears are more likely to be killed by ungulate hunters than near settlements. More emphasis on use of bear spray instead of rifles, use of portable electric fencing around camps and hanging game, and clean camping and game storage should be stressed.

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