CHAPTER 5
POPULATION CHARACTERISTICS

5.1 GRIZZLY BEAR DEMOGRAPHICS IN AND AROUND BANFF NATIONAL PARK AND KANANASKIS COUNTRY, ALBERTA

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ABSTRACT

The area in and around Banff National Park (BNP) in southwestern Alberta, Canada, is one of the most heavily used and developed areas where grizzly bears (*Ursus arctos*) still exist. During 1994–2002 we radiomarked and monitored 37 female and 34 male bears in this area to estimate rates of survival, reproduction, and population growth. Annual survival rates of bears other than dependent young averaged 95% for females and 81–85% for males. Although this area was largely unhunted, humans caused 75% of female mortality and 86% of male mortality. Females produced their first surviving litter at 6–12 years of age ($\bar{x}$ = 8.4 years). Litters averaged 1.84 cubs spaced at 4.4-year intervals. Adult (6+ year-old) females produced 0.24 female cubs per year and were expected to produce an average of 1.7 female cubs in their lifetime, based on rates of reproduction and survival. Cub survival was 79%, yearling survival was 91%, and survival through independence at 2.5–5.5 years of age was 72%, as no dependent young older than yearlings died. Although this is the slowest reproducing grizzly bear population yet studied, high rates of survival seem to have enabled positive population growth (λ=1.04, 95% CI = 0.99–1.09), based on analyses using Leslie matrices. Current management practices, instituted in the late 1980s, focus on alleviating human-caused bear mortality. If the 1970–80s style of management had continued, we estimated that an average of 1 more radiomarked female would have been killed each year, reducing female survival to the point that the population would have declined.

Human-caused mortality and habitat competition undermine grizzly bear populations, especially along the southern and eastern edges of their distribution (McLellan 1998). Today most adult grizzly bear mortality is human-caused even in the absence of hunting (Benn 1998, McLellan et al. 1999). Grizzly bear mortality is directly linked to the rate of contact with people and the potential lethality of each encounter (Mattson et al. 1996); the former corresponds to numbers and distribution of people, and the latter to their attitudes and behavior (Kellert et al. 1996). Along the edges of their range, grizzly bears more regularly encounter humans and human developments. The ability of grizzly bear populations to withstand these conditions is related both to the extent of human-caused mortality and the bears' rate of reproduction, which can vary enormously across their range with varying availability of food (Ferguson and McLoughlin 2000). In general, grizzly bears show a lack of resilience, behaviorally and demographically, to anthropogenic disturbance (Weaver et al. 1996).

Alberta represents the southeastern edge of grizzly bear distribution in Canada (McLellan 1998). Although grizzlies once occupied all of Alberta, they were extirpated from the eastern grassland portions of the province by around 1890 (W. McCrory and S. Herrero. 1982. A review of the historical status of the grizzly bear in Kananaskis Country, Alberta. Alberta Fish and Wildlife Division, Calgary, Alberta, Canada). Today they are limited to roughly the western third of the province. Here, much of their primary range lies within the Central Rockies Ecosystem, encompassing BNP and adjacent Alberta provincial lands, and extending into British Columbia, including Kootenay and Yoho National Parks and adjoining lands under provincial jurisdiction (Benn 1998, Gibeau et al. 2001). Outside parks, grizzlies may be exposed to legal hunting, and they also face increasing pressures from land use activities associated with extraction of coal, oil, gas and timber, production of livestock and agricultural crops, and construction of new homes and roads. No reliable estimates exist for the present number of grizzly bears in Alberta, but they are categorized as may be at risk (Kansas 2002) and are being considered for reclassification as threatened.

Our study, part of the Eastern Slopes Grizzly Bear Project (ESGBP), began in 1994 in response to mounting development pressures and a dearth of information regarding the status of grizzly bears in and around the Bow River Watershed (BRW), the most intensively used portion of the Central Rockies Ecosystem (Herrero 1994, Herrero et al. 1998; Fig. 1). Previously completed ESGBP research involved grizzly bear mortality, movements, distribution, and habitat considerations (Gibeau 2000, Gibeau et al. 2001, Benn and Herrero 2002, Mueller et al. 2004).

In this phase of the ESGBP research we examined demographic attributes, including: (1) rates and causes of mortality, (2) reproductive rates, and (3) population growth rate. We used these results to evaluate current management policies and to develop recommendations for continued population monitoring and management. Our study was prompted by the concerns of management agencies related to maintaining non-declining grizzly bear populations in the face of increasing land use.
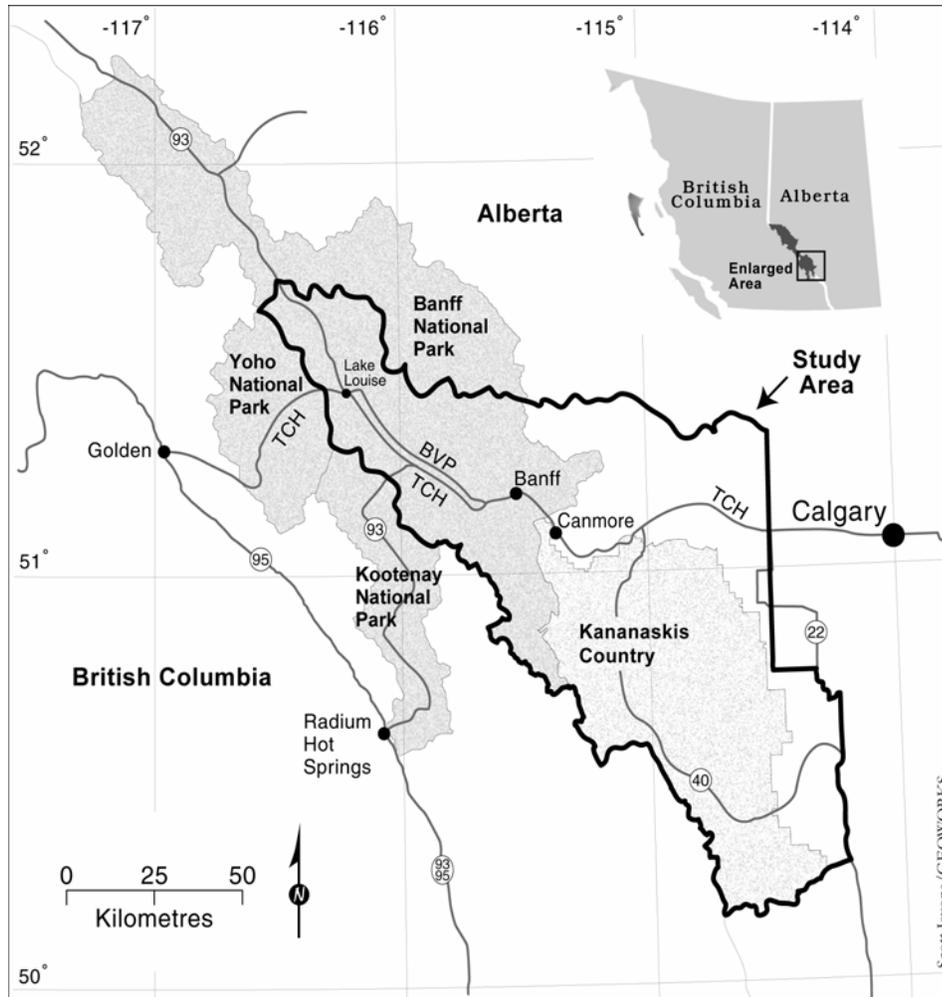

Figure 1. Study area in the Bow River Watershed, Alberta, encompassing parts of Banff National Park and Kananaskis Country, where grizzly bears were caught and radiomarked during 1994–2002.

STUDY AREA

Our 11,400-km² study area, situated 50–180 km west of Calgary, in southwestern Alberta (51°N, 115°W), encompassed the watershed of the Bow River from its source in the Rocky Mountains to approximately where it meets the prairies. Gibeau et al. (2001) and Chruszcz et al. (2003) described the biophysical features of this area.

The area included roughly half of BNP and all of the adjacent Alberta Provincial land known as Kananaskis Country plus other Alberta Provincial land (Fig. 1). Kananaskis Country is a multiple-use area about half of which is designated as provincial parks and the rest as forest lands or recreational areas. Grizzly bear hunting was prohibited throughout the study area, but ungulate and carnivore hunting occurred outside

of BNP, and bears were exposed to hunting when they traveled outside the BRW. Under the authority of treaty agreements, native people also could kill bears whenever and wherever they chose, outside national parks. Less than 100 bears were thought to reside within the BRW (P. I. Ross. 2002. Update COSEWIC status report on the grizzly bear *Ursus arctos* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada). All study bears were initially trapped within this area, but were monitored over a broader area of approximately 20,000 km^2.

Human presence is widespread both within and outside BNP. Three towns, Banff (population 7,700), Lake Louise (population 2,000), and Canmore (population 10,800) are world-renowned tourist destinations that attract approximately 4 million visitors annually (Gibeau 2000). Calgary, a rapidly growing and affluent city of 900,000, is <2-hr drive from most roaded portions of the study area. Major developments in the study area include a transcontinental railway, numerous hotels, campgrounds and picnic areas, 5 golf courses, 5 downhill ski facilities, and an extensive system of hiking, biking, and equestrian trails. For an area that still supports a population of grizzly bears, the BRW has an unprecedented network of well-traveled roads (Gibeau and Herrero 1998), including the Trans Canada Highway (TCH), a major transportation route that bisects the study area (Fig. 1). In all, the BRW is one of the most intensively developed landscapes in the world where a grizzly bear population still survives (Gibeau 2000, Chruszcz et al. 2003).

Beginning in the late 1980s and continuing through this study, a host of measures were instituted to afford grizzly bears in the BRW greater protection from human-caused mortality (Parks Canada 1997, Herrero et al. 2001). Bear-car collisions were reduced by highway fencing, under- and over-passes, spacing opposing lanes of traffic, and lowering speed limits (Clevenger and Waltho 2000; A. P. Clevenger, B. Chruszcz, K. Gunson, and J. Wierzchowski. 2002. Roads and wildlife in the Canadian Rocky Mountain Parks – movements, mortality and mitigations. Final report to Parks Canada, Banff, Alberta, Canada). Aversive conditioning (e.g., rubber bullets), instead of killing or removal, was applied more often toward bears that frequented areas near human developments or roads. Educational programs were offered to visitors to help modify human behaviors that could put bears at risk, and in some cases people were restricted from using certain areas when bears were observed in the vicinity (Gibeau et al. 2002). In front-country areas, major changes were made in garbage storage and collection procedures (Benn and Herrero 2002), and some proposed developments were altered and others averted largely because of potential adverse effects on grizzly bears (Natural Resources Conservation Board. 1993. Decision report. Application to construct a recreational and tourist resort project in the town of Canmore, Alberta. Application 9103 – Three Sisters Golf Resorts Inc. Natural Resources Conservation Board, Government of Alberta, Edmonton, Alberta, Canada; Herrero et al. 1998).

METHODS
Field Methods

During 1994–2002 we captured and radiomarked 69 grizzly bears; 2 other bears initially radiomarked in 1993 also were included in our study. All but 1 bear were captured in either BNP or Kananaskis. Most trapping was conducted during the spring when bears were concentrated at low elevations. Traps were set in places that, judging from the habitat and terrain, appeared favorable for grizzly bears. As radio transmitters neared the end of their expected lifespan (1–3 years, depending on the type), bears were targeted for recapture and radio replacement; however, recapture success varied, so monitoring of some bears ceased before the end of the study.

We captured bears in culvert traps or Aldrich foot snares using protocols outlined by Jonkel (1993), or in some cases darted them from the ground or a helicopter. Trapping effort was expended equally between remote areas, accessible only by foot or horseback, and vehicle accessible areas. Four bears that were captured in management-related activities (i.e., problem bears) were also radiomarked and included as part of this study.

Bears were immobilized with Telazol® at 7-9 mg/kg (Taylor et al. 1989), and then measured and weighed. We recorded condition of the mammae (lactating, non-lactating but developed, undeveloped) and vulva (degree of swelling) of female bears as an indication of their reproductive status. A first premolar was extracted for age estimation (Matson's Laboratory, Milltown, Montana, USA) based on cementum analysis

(Craighead et al. 1970). Capture and handling methods met the standards of the Canadian Council on Animal Care.

We equipped individuals with either a conventional radiocollar (Lotek Engineering, Newmarket, Ontario, Canada) or an ear-tag transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA). All radiocollars included a breakaway cotton spacer to ensure that they would not be worn permanently (Hellgren et al. 1988). Transmitters were motion sensitive, changing pulse rate after 7 hr of inactivity (mortality mode), indicating that the transmitter had been shed or the bear had died. We located radiomarked bears at approximately weekly intervals from the air and every 1–3 days from the ground. Rugged mountain topography limited ground-based searches to areas adjacent to roads and trails.

We obtained bear mortality data from 2 sources. If the pulse rate of a transmitter switched to mortality mode, we went to the site to conduct a ground search, and either located a dropped transmitter or a dead bear. In the case of a dead bear, we examined the carcass and the surrounding area in an attempt to determine the cause of death. Bears killed as problem wildlife, or by hunters (illegally, in some cases), were reported to, and investigated by, Conservation Officers, who later relayed the information to us.

We obtained information on cub production and survival through visual observations during radiotracking of adult females. Cubs (0–1 year old) were differentiated from older offspring based on their size and the reproductive status of the mother the previous year. We did not estimate ages of offspring older than cubs unless they were seen initially as cubs. Cub litter sizes were generally determined by late spring, so our data excluded cubs that died early in the season. Whole litters of cubs or yearlings (1-year-olds) no longer seen in the vicinity of their mother were considered dead. Similarly, we inferred death of individual offspring when a litter declined in number, and the reduced litter size was confirmed on later telemetry flights. We typically did not know the sex of offspring unless they were captured.

Estimation of Survival

We estimated survival rates of adult and subadult bears using the Kaplan-Meier (product-limit) estimator adapted for staggered entry (Pollock et al. 1989). We used half-months as the monitoring interval, and considered bears part of the monitored sample only when the signal from their radio transmitter could be detected on routine telemetry flights during that interval. As radios expired or fell off, the animals were censored. There was no indication that censoring was non-random (Tsai et al. 1999). Oftentimes, though, no definitive evidence existed that a radio had expired; we judged radios to have expired if near or after the end of their expected lifespan they could no longer be heard. If a radio signal disappeared well before the expected expiration of the transmitter batteries, and the bear previously had been located in proximity to an area of human activity, we recorded the bear as a suspected but unconfirmed human-caused mortality. These were treated in one analysis as deaths and in a separate analysis as censored observations (expired radio not associated with death). Radiomarked young bears still in association with their mother were entered into the survival analysis upon their independence, at whatever age ($\geq$2 years) that occurred.

We calculated survival separately for each year of the study and tested for yearly differences using a log-rank test. Finding no yearly differences, we calculated an overall average annual survival in 2 ways. First, we calculated cumulative survival through the duration of the study, and exponentiated this by the inverse of the number of years of monitoring (i.e., 1/8.5). A problem with this method is that by chance a large proportion of animals could die during periods when the number of radiomarked animals was small, thus sharply reducing cumulative survival from that point forward. To avert this difficulty, and to increase sample size within monitoring intervals, we collapsed the data into a single calendar year (pooled years analysis), a common practice in studies of a variety of species (e.g., Sorensen and Powell 1998, Bennetts and Kitchens 1999, Conner 2001). We made separate estimates of survival for subadults (post independence from mother through 5 years old) and adults ($\geq$6 years old) of each sex. Confidence intervals were calculated using equations from Pollock et al. (1989).

We tested whether survival curves differed by sex, age (adult versus subadult), area (inside versus outside BNP), and habituation to humans (habituated versus wary) using log-rank tests. We also evaluated the effect of each of these factors, as well as home range size (95% fixed kernel) as a continuous variable, by including them as covariates in a Cox proportional hazards regression. In all cases, cumulative and pooled

years analyses yielded significant differences for the same comparisons, so for clarity we report test statistics only for pooled data.

We classified individuals as park or non-park bears based on whether the predominance of their home range was within or outside BNP. All bears were easily categorized, as all home ranges were either predominantly in or outside the park. We classified bears as either habituated or wary following Mattson et al. (1992). Bears that maintained ranges near humans but did not tolerate close human presence were not considered habituated. There were no food-conditioned bears in our sample.

In an initial global Cox model, the interactions of sex–age and sex–habituation were significant, so we stratified proportional hazards regressions on sex. We obtained the relative risk of each factor (e.g., a risk ratio of 2.0x means a bear in this category was twice as likely to die) and the 90% CI associated with each risk ratio. Confidence intervals on risk ratios that did not include 1.0 indicated statistical significance (Riggs and Pollock 1992). We report risk ratios only when they were significant and when plots of hazard functions for the strata being compared appeared proportional (Riggs and Pollock 1992).

To assess the effects of different types of mortality, we categorized causes as either natural, human-caused accidental, or human-caused purposeful. We calculated cause-specific mortality rates by considering 1 cause at a time and treating deaths from all other causes as censored observations (Pollock et al. 1989). Bears that we suspected of having died when we lost contact with their radios were, in this analysis, considered purposeful human-caused mortalities; if these had been natural deaths there should have been no reason for their radios to stop functioning, and if they had been hit by a car or train, we would have learned of such.

We reviewed records of encounters between people and radiomarked bears, and judged, in each case, whether the bear would have been killed, had the policy toward grizzlies both within and outside BNP not been changed shortly before and during the early years of our study. We were able to forecast the outcomes of policies from a previous era because one of us (MLG) has worked as a warden in BNP since 1976 and thus has been directly involved in judgments regarding the disposition of problem bears.

Estimation of Reproductive Parameters

We determined ages of first reproduction only for females that were captured and radiomarked as subadults and monitored until they produced a litter. The minimum known age of first reproduction was 6 years old, so bears caught at or before this age could be included in this sample. Some first litters may have been lost before we detected them, but we were able to observe all surviving litters born to radiomarked females, and hence obtained a better estimate of the age that females produced their first litter that survived ≥1 year. Moreover, we could backfill (infer) the birth of surviving cubs 1–2 years previously for bears first captured at age 7 or 8 based on whether they were accompanied by cubs, yearlings, 2-year-olds, or no offspring at the time of capture. All surviving cubs remained with their mother for ≥2.5 years, so 7 or 8-year-old bears without offspring could not have previously produced surviving cubs.

We followed the procedure outlined by Garshelis et al. (1998) to estimate mean and median ages of first reproduction. This procedure entails calculating the proportion of females of each age that produced a first litter (or first surviving litter) among all monitored females of that age that had not previously produced. These proportions are then weighted by the proportion of females in the population available to have a litter at each age. This method is exactly the Kaplan-Meier time-to-event estimator typically used in survival analysis. All bears were entered into the analysis at age 6 (some being backfilled to this age) and were either observed to produce cubs or were lost from monitoring before they produced (right censored). Excluding censored records would have resulted in a low-biased estimate (Garshelis et al. 1998). We obtained confidence intervals by jackknifing, bootstrapping, and from standard Kaplan-Meier variance formulations (Hosmer and Lemeshow 1999). Whereas all these methods returned similar results, we present the most conservative (widest CIs), because small samples often yield underestimated variances in Kaplan-Meier analyses (Klein and Moeschberger 2003:100)

We used an analogous procedure to estimate the average interval between litters. However, unlike age of first reproduction, each female bear can have multiple litter intervals, so we treated each interval, rather than each female, as the sample unit. We examined each female's reproductive record chronologically and tallied the number of years from production of a litter (or surviving litter) to production of another litter. If a

record ended during a period between litters (right censored), we used the data up to that point. We tallied the number of monitoring periods of at least 1 year, 2 years, 3 years, and so on following a litter, and then calculated the proportion of monitoring periods of each length that yielded a litter.

Mean cub litter size (after den emergence) was calculated using observed litters as the sample unit. We included only litters that were first observed during their cub year. We made a separate calculation of yearling litter size that included all yearling litters, regardless of whether they were observed as cubs.

We estimated survival of dependent young by following fates of litters of radiomarked mothers through time. We treated individual cubs as the sample unit and estimated first-year survival as the number surviving to 1 year divided by the number monitored. Unlike survival estimates for radiomarked bears, no censored data existed with cubs because we were quite certain that their disappearance represented death. However, we excluded cubs that were not monitored into their yearling year because their mother's radio had expired or she died. Hence, our estimate pertains to cubs that were not orphaned. We estimated yearling survival and survival of older dependent young using the same procedure. Confidence intervals were obtained by jackknifing.

We recorded ages that young bears became independent of their mother only for litters that were first observed as cubs because we could not reliably determine the age of older dependent offspring. Because all offspring in a given litter left at the same time, we used litter as the sample unit for estimating mean age of independence. We assumed that independence from the mother occurred when all ≥2-year-old littermates were not seen near their mother after mid-summer.

We estimated reproductive rates of each bear by dividing the number of female cubs it produced (assumed to equal total cubs/2) by the total number of years it was monitored as an adult (≥6 years old). When considering just surviving cubs, we included backfilled reproductive data, as explained earlier. On a spreadsheet, with each row being the reproductive history of an individual bear, we aligned rows so that columns represented the bear's age, and then calculated age-specific reproductive rates as female cubs/adult females. We used the same approach, with columns as years (1994–2002), to calculate year-specific reproductive rates.

Overall reproductive rate (all adults, all years) was calculated by dividing the sum of female cubs produced by the total adult bear-years (bears · years) of monitoring (method 1 of McLellan 1989). The mean number of female cubs produced (among all adult females) divided by the mean number of years monitored yields the same value (since the mean in both numerator and denominator is just the sum divided by the number of adult females), and enables estimation of variance based on a Taylor's series expansion:

$$\text{Var } (c/y) \approx (\mu_c/\mu_y)^2 \cdot (\text{var } c/\mu_c^2 + \text{var } y/\mu_y^2 - 2\text{cov } (c,y)/(\mu_c \cdot \mu_y)),$$

where c is the number of cubs produced, y the number of years monitored, and μ_c and μ_y the means of these, respectively (Mood et al. 1974:181). Confidence intervals were generated from this variance, as well as from jackknifing and bootstrapping (10,000 resamplings), all of which returned nearly identical results.

Estimation of Population Growth

We estimated population growth (λ) using a deterministic Leslie matrix (Leslie 1945, 1948). We arranged the Leslie matrix as 28 rows and columns representing each age from 0 (cubs) to 27 years old. We considered 27 the age of reproductive senescence (Schwartz et al. 2003), which in the matrix analyses was equivalent to all bears dying at this age. We arranged the data as occurring after the birth pulse (so-called post-breeding census), given that the cub counts were made in spring and summer, after some mortality of cubs (born in January or February) had already occurred. Consequently, we calculated the top row of fecundities as the survival rate for bears of that age multiplied by the reproductive rate (female cubs/female) of bears of the next age (Jenkins 1988, Noon and Sauer 1992, Williams et al. 2002). We conducted one series of analyses in which all bears ≥6 years old were presumed to have the same average reproductive rate, and a second set of analyses in which we assigned age specific reproductive rates for 6, 7, 8 and 9-year-old bears, and combined 10–26 year olds.

The diagonal elements in the Leslie matrix represent survival rates. The first element (in the second row of the first column) corresponded to survival of cubs to age 1. This value was derived as the product of cub survival and adult female survival to account for cubs dying as a result of their mother dying, since first-year cubs were typically not self-sufficient. Yearlings were also reliant on their mother, but we suspected that

some orphaned yearlings could survive on their own. In the absence of data on survival of orphaned yearlings, we made the assumption that their survival was only half that of yearlings raised by their mother. This assumption was made for completeness, but actually had little effect because adult female survival was so high that few yearlings (4–5%) were orphaned. Two-year-olds were a more complicated situation because some became independent at this age and others remained with their mother. We split 2-year-olds into these 2 groups in the proportions observed. We assigned the survival rate observed for older subadults to 2-year-olds that had become independent, either by leaving their mother or by their mother dying. The remainder were given the observed survival rate for dependent 2-year-olds (1.0). Although some bears continued to stay with their mother past age 2, we considered all 3–5-year-olds to have the same rate of survival. Likewise, all bears aged 6–26 were given the same survival rate.

An estimate of the asymptotic population growth rate (λ at a stable age distribution) was calculated as the dominant eigenvalue of the Leslie matrix, using the POPTOOLS add-in (www.cse.csiro.au/cdg/poptools) to an Excel spreadsheet. We also used this software to obtain estimates of the ultimate stable age distribution (right eigenvector), sensitivities and elasticities of the matrix elements, mean lifetime reproductive output (R_o), and mean generation time (T), as explained by Caswell (2001).

We conducted matrix projections using various combinations of input parameters: survival of adult and subadult females based on only known mortalities versus survival including suspected mortalities; age-specific reproductive rates versus a single reproductive rate for all adults combined; and reproductive rates and rates of cub and yearling survival based on all litters versus just litters that survived their first year. These generated 8 separate estimates of λ, R_o, and T. We performed these analyses using multiple approaches to increase robustness of the results, as samples were not large so parameter estimates could vary with sampling error and assumptions regarding treatment of the data.

Confidence intervals on λ estimates were obtained both by bootstrapping (5,000 resamplings) and jackknifing. Although these 2 approaches generally yield equivalent results (Meyer et al. 1986, Shao and Tu 1995), we favored jackknifing because it deselects 1 bear at a time, enabling examination of each individual's contribution to the population growth rate. We performed bootstrapping as a check on the jackknifing results because the distribution of jackknife pseudovalues was highly skewed. We also partitioned bootstrapped results to examine probabilities of the estimated λ indicating an increasing, decreasing, or stable population.

We extended the projection matrix to incorporate males, which we presumed would also live until 27 years old. Thus, we added 27 columns to the right and 27 rows beneath the previous matrix. Male age-specific survival rates were entered into the matrix on the same diagonal as females, in the lower right quadrant. We doubled the reproductive rate along the top row, because females were now producing male as well as female offspring; however, female cub survival was halved, and the other half became male yearlings. We considered males to have no effect on reproduction or survival of females, and hence no effect on population growth rate. We included them only to gauge their composition in the population at a stable sex-age distribution. This was analogous to the source (female) – sink (male) metapopulation models presented by Caswell (2001:90-92).

RESULTS
Survival

Survival rates were estimated from data obtained on 37 female and 34 male radiomarked bears. Fifteen females and 14 males were radiotracked as subadults, of which 8 and 4, respectively, were monitored into adulthood. Independent bears of every age, 2–27 years old, were included in the dataset. Twelve females and 4 males were monitored for at least 5 years. Females were monitored for an average of 44 months and males for an average of 21 months.

Seven females (5 adults, 2 sudadults) were known to have died during the study, 1 in June and 6 during August–September. Two died of natural causes (1 killed by another bear in a berry patch, 1 fell down a cliff), 2 were hit by a train, 1 was shot by a person in self-defense, 1 was legally killed by a Treaty Indian, and 1 was translocated out of the study area where it was legally killed 11 months later on Treaty Indian lands (however, this bear was considered lost from the population when it was moved). The radio signals of 15 females were lost as a probable consequence of radio failure, and the records of these bears were censored at

that time. One other radio signal from an adult female disappeared during August for unknown reasons, possibly related to the bear having been killed.

Eleven males (6 adults, 5 subadults) were known to have died or were otherwise removed from the population. Only 1 died of natural causes (killed by another bear at an elk carcass), 1 was shot in self-defense, 1 was legally killed by a Treaty Indian, 1 was legally hunted, 2 were killed illegally, 3 were killed as nuisances, and 2 other nuisance bears were captured and removed from the population. Fourteen males were censored after probable radio failure, and 2 others were considered possible deaths after loss of their radio signals. All deaths and suspected deaths occurred during May–October.

Annual survival of adult females was estimated at 96% based on the 5 known mortalities and 95% based on the known and single suspected mortality, using either method of calculation (Table 1). Subadult female survival was estimated at 91–92%. Survival rates of adult and subadult females were not significantly different ($\chi^2 = 0.5$–0.9, depending on inclusion of suspected mortalities, df = 1, $P = 0.3$–0.5).

Adult male survival was estimated at 86–89%, depending on method of analysis and inclusion of a suspected mortality, and subadult male survival was estimated at 69–73% (Table 1). When suspected mortalities were included, subadult males had lower survival than adults ($\chi^2 = 4.0$, df = 1, $P = 0.04$).

Pooling adults and subadults of each sex, females had significantly higher survival than males (Table 1), either counting ($\chi^2 = 8.3$, df = 1, $P = 0.004$) or discounting suspected mortalities ($\chi^2 = 6.8$, df = 1, $P = 0.009$). Risk of mortality for males was 2.9–3.1x higher than for females (90% CI: 1.4–6.5). Just comparing adults, males had a 2.7x greater risk of mortality (90% CI: 1.1–7.2, $P = 0.07$).

Yearly survival varied from 89% to 100% for females and 55% to 100% for males. Yearly variation in survival of females and males were not related ($r = 0.07$, df = 8, $P = 0.85$) and no significant yearly effects were discerned for either sex, including or excluding suspected mortalities (F: $\chi^2 = 6.5$–8.9, df = 8, $P = 0.4$–0.6; M: $\chi^2 = 7.3$–8.6, df = 8, $P = 0.4$–0.5).

Among adult and subadult females (pooled), mortality due to purposeful killing by humans (2.7%, 95% CI: 0–5.4%) equaled mortality due to natural and accidental causes combined (2.7%, 95% CI: 0–5.4%). The rate of natural mortality alone was only 1.3% (95% CI: 0–3.3%). For males, purposeful human-caused mortality (17.7%, 95% CI: 8.1–27.3%) far outweighed natural mortality (3.0%, 95% CI: 0–7.6%). If purposeful human-caused mortality were eliminated and not compensated for by other forms of mortality, both male and female survival (combined ages) would increase to 97%. Including both purposeful and accidental events, humans were responsible for 75% of female mortality and 86% of male mortality.

Rates of human-caused mortality, both purposeful and accidental, did not relate to whether bears lived mainly in or outside the park, or the size of their home range. Neither of these factors added significantly to the Cox proportional hazards model. All natural and accidental human-caused mortalities occurred within BNP, but overall survival rates were similar between bears that lived within and outside the park, for both females (all ages: 94–96% within the park, range related to 1 indefinite mortality, $n = 23$; 94% outside the park, $n = 14$) and males (85–87% within, $n = 13$; 81–83% outside, $n = 21$).

Human-caused mortality of habituated ($n = 3$ of 6) and non-habituated ($n = 7$ of 28) male bears did not differ, although our sample of habituated bears was small. Among females, 31% of habituated bears (4 of 13) but only 4% of non-habituated bears (1 of 24) were known to have died of human-related causes; these samples also were small, but nevertheless suggested an increased risk of human-related death for habituated females ($\chi^2 = 2.7$, df = 1, $P = 0.1$).

We estimated that 6 more adult and 2 more subadult radiomarked females would have died, and 2 adults and 2 subadults that did ultimately die would have died earlier had the old system of bear management continued during our study. By contrast, we estimated that only 2 more adult and 1 more subadult radioed males would have died under this less protective management system. If this had occurred, then survival rates for adult females (91–92%) would have been similar to adult males (84–86%, $P = 0.3$–0.4), and subadult females (84%) would have been more like subadult males (65– 69%, $P = 0.06$–0.12).

Table 1. Survival of radiomarked bears in the Bow River Watershed, Alberta, 1994–2002, based on Kaplan-Meier estimates cumulative through all study years versus all years pooled together as 1 year.

Sex	Age[a]	Inclusion of known/suspected mortalities	No. individual bears[b]	Bear-years	Mortalities	Annual survival (95% CI)	
						Cumulative	Years pooled
Female	Adult	Known	30	115.8	5	0.96 (0.92–1.00)	0.96 (0.92–1.00)
		Known + suspected			6	0.95 (0.91–0.98)	0.95 (0.91–0.99)
	Subadult	Known[c]	15	18.7	2	0.91 (0.73–0.98)	0.92 (0.79–1.00)
	All	Known	37	134.6	7	0.95 (0.92–0.98)	0.95 (0.92–0.99)
		Known + suspected			8	0.95 (0.91–0.98)	0.95 (0.91–0.99)
Male	Adult	Known	24	46.3	6	0.88 (0.78–0.95)	0.89 (0.80–0.99)
		Known + suspected			7	0.86 (0.75–0.93)	0.87 (0.77–0.97)
	Subadult	Known	14	14.2	5	—[d]	0.73 (0.53–0.94)
		Known + suspected			6	—[d]	0.69 (0.48–0.90)
	All	Known	34	60.4	11	0.85 (0.76–0.91)	0.85 (0.76–0.94)
		Known + suspected			13	0.82 (0.73–0.88)	0.81 (0.71–0.91)

[a] Adult: ≥6 years old; subadult: post-independence from mother to 5 years old; all: adults and subadults combined.
[b] Number of bears of all ages is less than adults + subadults because some individuals were monitored from subadult to adulthood.
[c] No suspected deaths for subadult females; all deaths were confirmed.
[d] Estimate reduced to zero by the death of all radioed bears during some sampling periods.

Reproduction

Reproductive Age. — Reproductive data were obtained from 30 female bears aged 6–27 years old during the study period. No bears <6-years-old produced cubs. We observed 143 bear-years of reproductive information on adult-age animals, and were able to infer another 12 bear-years of prior reproductive history.

Five of 11 6-year-olds, 3 of 4 nulliparous 7-year-olds, and 1 of 1 nulliparous 8-year-olds had their first litters, yielding an estimated mean age of first reproduction of 6.7 years (95% CI = 6.1–7.2, median = 6.6 years). The conventional estimate, counting just the 9 bears with observed first litters, was 6.6 years. The mean age of first production of a surviving litter was 8.4 years (95% CI: 7.2–9.8, range 6–12, median = 7.5 years), based on 13 bears whose first production of a surviving litter was observed, and 4 adults that were lost before their age of successful cub production could be ascertained (Table 2).

Litter Size and Survival. — Overall litter size averaged 1.84 cubs ($n = 38$, 95% CI: 1.64–2.04, range = 1–3); litters that survived their first year averaged 1.94 cubs ($n = 33$, 95% CI: 1.73–2.15). These values include multiple (2–4) litters for some females; however, averages calculated from the mean litter sizes of each mother ($n = 23$) were not appreciably different (1.79 for all litters; 1.90 for surviving litters). Yearling litter size averaged 1.84 ($n = 23$, 95% CI: 1.58–2.10).

Table 2. Calculation of average age of first production of a surviving litter[a] for female grizzly bears in the Bow River Watershed, Alberta, 1994–2002. The conventional estimate, derived by averaging the ages of observed first reproduction, is less than the estimate that includes females that were lost from the sample before they had a chance to produce.

Age (yr)	No. nulliparous females observed	No. producing cubs	No. nulliparous females not observed at next age	Nulliparous females producing (%)	Percent of population available to produce 1st cubs	Percent of population producing 1st cubs	Age weighted by percent producing 1st cubs
6	17	2	1	11.8	100.0	11.8	0.71
7[b]	14	6	1	42.9	88.2	37.8	2.65
8	7	2	1	28.6	50.4	14.4	1.15
9	4	1	0	25.0	36.0	9.0	0.81
10	3	1	1	33.3	27.0	9.0	0.90
11	1	0	0	0	18.0	0	0
12	1	1	0	100.0	18.0	18.0	2.16
Sum		13	4			100.0	8.38
Mean		7.77					8.38

[a] Loss of whole litters that occurred early in the year were often difficult to detect, so mothers' ages of first birthing were less certain than their ages of first production of cubs that survived at least 1 year.

[b] Example calculation: 14 nulliparous 7-year-olds were observed, of which 6 (42.9%) produced cubs. Among those that did not produce at this age, 1 was lost from the observed sample, so only 7 nulliparous females were observed at age 8. Since the earliest age of first cub production was 6, 100% of females were available to produce at this age; 11.8% did so, so the remaining 88.2% were available to produce their first cubs at age 7; 42.9% of this 88.2% produced, so 37.8% of all females in the population produced first cubs at age 7. Multiplying 7 years x 37.8% yields the value in the last column (2.65). These are summed to obtain an estimate of the average age of production of the first successful litter. Tabulated values are rounded for clarity.

We obtained an accurate count of cubs early in the year for 4 mothers' nonsurviving first litters: 3 were singles and 1 was twins, averaging 1.25 cubs/litter. First surviving litters were larger: 2 were singles, 10 were twins, and 1 was triplets, averaging 1.92 cubs/litter ($t = 2.37$, df = 15, $P = 0.02$, 1-tail). Litter size was similar for 22 litters that were not the mother's first surviving cubs: 6 were singles, 12 were twins, and 4 were triplets, averaging 1.91 cubs/litter.

Individual cub survival was 79% (42 of 53; 95% CI: 67–93%) considering all litters and 89% (42 of 47; 95% CI: 81–97%) for litters in which at least 1 cub survived. Cub survival was 60% (9 of 15 cubs) for mothers' first litters and 87% (33 of 38) for subsequent litters ($\chi^2 = 4.7$, df = 1, $P = 0.03$). Of 10 known first litters, 5 (50%) were completely lost during the first year. Only 1 other complete litter was lost the first year, a single cub born to a 22-year-old female.

Yearling survival was 91% (29 of 32; 95% CI: 80–100%). The only 3 yearlings that died were ones that were part of a litter in which a sibling cub had already died, so in these 3 cases the original litter size of 2 was reduced to zero by the end of the second year. None of the 12 2-year-olds that stayed with their mother died, nor did any of the 5 dependent 3-year-olds or 2 dependent 4-year-olds. Overall survival of cubs until independence was thus cub survival multiplied by yearling survival, or 72% (95% CI: 55–91%) for all litters, and 81% (95% CI: 65–97%) for litters that survived, at least in part, their first year. Of 29 litters observed as cubs and for which we could determine their ultimate fate, 9 (31%) were entirely lost, 2 (7%) were reduced in size, and the rest (62%) survived intact.

All 6 cub litters that did not survive to their yearling year lived within BNP. Nevertheless, overall survival rate of offspring was similar for mothers inside and outside the park, as was the average number raised in each litter through at least their yearling year, and hence presumably to independence (1.3 offspring/litter for mothers in the park, 1.4 for bears outside the park).

Cubs from 6 of 12 litters (50%) left their mother at 2.5 years old, 3 left at 3.5, 1 at 4.5 and 1 at 5.5 years. Another litter stayed with the mother for at least 3.5 years, at which time the mother's radio failed and we lost track of her and her offspring. The average age of independence from the mother (counting the litter censored at 3.5) was 3.4 years. Four of the 6 litters that left their mother at 2.5 years old were originally litters of twins, and 3 of the 6 litters that left at >2.5 years old were originally twins. We also observed family break-up for 5 litters of unknown age. Including these, litter size at independence averaged 1.88 ($n = 17$, 95% CI: 1.59–2.17); this value exceeds the mean cub litter size because it excludes litters that had been reduced to zero.

Interval between Litters.— The average interval between litters was 4.4 years (95% CI: 3.3–5.4) considering all litters and 4.5 years (95% CI: 3.4–5.6) including only litters that survived their first year. Ten bears produced litters at an interval of 3 or 4 years, and 3 produced litters that were 6–8 years apart. Two intervals of <3 years followed a litter of cubs that died; 1 mother had cubs the very next year (1 year interval) and another produced a new litter 2 years later. These 13 (or 15 if the last 2 are included) cases, involving 12 (or 13) individual bears, were the only completed litter intervals observed during our 9-year study. However, we also observed 23 open-ended intervals, some beginning with a litter but with no observed subsequent litter due to the mother's death, failing of her transmitter, or the study ending (all right censored cases), and some where the mother was first radiomarked during an interval between births (left censored). We included only the right-censored open-ended intervals in estimating the average interval between litters (Table 3). Excluding non-surviving litters, the mean litter interval for bears within the park ($n = 7$ known and 8 open-ended intervals) averaged 5.0 years (95% CI: 3.1–6.9), compared to 4.0 years (95% CI: 2.9–5.1) for bears outside the park ($n = 6$ known and 3 open-ended intervals), but confidence intervals were wide and overlapping.

Reproductive Rate.— The population-wide reproductive rate was 0.239 (95% CI: 0.185–0.294) female cubs per 6+ year-old female/year considering all litters, and 0.213 (95% CI: 0.166–0.263) for litters that survived their cub year. Multiplying these values by the respective individual cub and yearling survival rates (calculated for all litters or just surviving litters), yielded (in both cases) an estimated rate of production of 0.172 female offspring reaching independence per adult female/year. That the same value was obtained whether considering all or just surviving litters stems from the fact that they were derived from nearly identical datasets, the former where mortality was considered in a single step, and the latter where whole litter loss and individual cub losses were considered in 2 separate steps.

Table 3. Calculation of average interval between surviving litters[a] for female grizzly bears in the Bow River Watershed, Alberta, 1994–2002. The conventional estimate, derived by averaging the observed reproductive intervals, is less than the estimate that includes intervals that remained open when the female was last observed.

Time period since last litter (yr)	No. periods observed	No. periods ending in cub production	No. incomplete periods not observed the next year	Observed periods ending in cub production (%)	Percent of all periods available to end in cub production	Percent of all available periods ending in cub production	Interval length weighted by percent producing
1	24	0	5	0	100.0	0	0
2	19	0	4	0	100.0	0	0
3	15	6	1	40.0	100.0	40.0	1.20
4[b]	8	4	1	50.0	60.0	30.0	1.20
5	3	0	0	0	30.0	0	0
6	3	1	0	33.3	30.0	10.0	0.60
7	2	1	0	50.0	20.0	10.0	0.70
8	1	1	0	100.0	10.0	10.0	0.80
Sum		13	11			100	4.50
Mean	4.23						4.50

[a] Litters in which ≥1 cub survived ≥1 year.
[b] Example calculation: Of 24 periods observed following the birth of a successful litter, none ended in production of another litter after 1–2 years, 6 ended in cub production after 3 years, and 10 were not followed beyond 3 years. Four of 8 observed periods (50%) ended with a litter after 4 years. Since the minimum litter interval was 3 years, 100% of periods following a litter could have ended in cub production after 3 years; 40% did so, so the remaining 60% of the periods could have ended in cub production after 4 years; 50% of this 60% terminated in cub production, so overall 30% resulted in the birth of another litter after 4 years. Multiplying 4 years by 30% yields the value in the last column (1.20). These are summed to obtain an estimate of the average interval between successful litters.

Among adult bears monitored for a sufficient time to assess their individual reproductive rates, the poorest reproducers included 2 bears that produced no surviving cubs in ≥5 years (#40, 63), 2 that produced only 1 litter (1–2 cubs) in 7 years (#41, 62), and 1 that produced 2 litters totaling 3 cubs 8 years apart (#46; Fig. 2). All of these bears lived within BNP.

Significant variation was observed in the percentage of adults that produced litters each year (range <5% to >40%; χ^2 = 17.3, df = 8, P = 0.03; 34% of χ^2 due to zero reproduction in 1997) and in yearly reproductive rates (which include litter size as well as the proportion of females producing; Kruskall-Wallis H = 17.4, df = 8, P = 0.03). To some extent, though, yearly variations in reproduction may be an artifact of bears not being available to produce cubs in consecutive years, or even 2 years apart in this population, unless their whole litter was lost. When we excluded adult females that were not available to produce because they were rearing 0–2-year-old offspring, yearly differences in reproductive rates were less evident (Kruskall-Wallis H = 13.5, df = 8, P = 0.09).

We detected no statistically significant age-related differences in reproduction among 6+ year-old bears. However, reproductive rates appeared especially high among 7-year-olds; 6 of 16 (38%) females monitored at this age produced a surviving litter, totaling 12 cubs or 0.38 female cubs/female (Fig. 2). At least 30% of females also produced litters at 6, 8, and 9 years old, but litter survival was lower. Grouping bears in age categories 6–9 (those producing mainly their first litters), 10–15, 16–21, and 22–26 years, 23%, 21%, 24%, and 20% of females, respectively, produced surviving litters/year.

Data were too sparse among old-aged bears to discern the probable age of reproductive senescence. One bear produced a nonsurviving litter at 22 years old and did not give birth during the following 2 years.

However, 2 other bears produced litters at age 23. One of these mothers was killed in mid-September, so we cannot judge what the fate of her cubs would have been. The other old mother successfully raised her litter of 2 cubs, which left her when she was 26 years old. Hence, her first opportunity for another litter was at age 27, but she did not produce then. Overall, the reproductive rate (counting just successful litters) for 20–26-year-olds (0.233 female cubs/female) was, if anything, higher than the reproductive rate for 10–19-year-olds (0.20). These data appear consistent with Schwartz et al's (2003) finding, from a compilation of studies of brown/grizzly bears, that senescence occurs at about 27 years of age.

Bear ID	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	F cubs	Yrs observ.	Repro rate
17					0	1	0	0	2	0												1.5	6	0.25
18	0	3	0	0	0	1	0	0														2	8	0.25
24	0	2	0	0	0	0	0	1														1.5	8	0.19
26												0	2	0	0	0	2					2	6	0.33
27	2	0																				1	2	
28																	✗	0	0			0	3	
30				3	0	0	0	0	0	0	0	3	0									3	9	0.33
31	0	0	2																			1	3	
32							0	3	0	0												1.5	4	0.38
33													0	3	0	0	2	0	0	0		2.5	8	0.31
36	0	0	✗	0	2	0	0	2	0	0	2											3	11	0.27
37					0	0	2	0	0	0	2	0	0									2	9	0.22
40									0	0	0	0	0	0								0	6	0
41						0	0	0	1	0	0	0										0.5	7	0.07
46					2	0	0	0	0	0	0	0	1									1.5	9	0.17
47	0	2	0	0	0	2	0	0	2	0												3	10	0.30
48	0	2	0																			1	3	
55	0	1	0	0																		0.5	4	0.13
56	✗	2																				1	2	
57	2	0	0	2																		2	4	0.50
59	0	0	✗																			0	3	
60	0																					0	1	
61						0	0	0														0	3	
62	0	0	0	0	0	0	2															1	7	0.14
63	✗	0	0	0	0																	0	5	0
64						0	0	0	0													0	4	0
65	0	0	1																			0.5	3	
66	✗	0																				0	2	
72	0	0	0	2																		1	4	0.25
88						0																0	1	
Σ F cubs	2	6	1.5	3.5	2	2	2	1.5	3.5	0.5	3.5	0	0.5	1	1.5	0	0	2	0	0	0	33		
Σ Adult F	17	16	13	10	12	10	12	12	9	9	7	5	5	3	3	2	3	3	2	1	1		155	
Repro rate	0.12	0.38	0.12	0.35	0.17	0.20	0.17	0.13	0.39	0.06	0.50	0	0.10	0.33	0.50	0	0	0.67	0	0	0			0.213

Age (yrs) across the top. Bottom totals: Sum | Sum | Overall.

KEY:
- **2** Observed no. cubs (both sexes) in a surviving litter
- ✗ Nonsurviving cub litter (litter size not shown)
- 0 Observed non-reproduction (mother with no offspring or with offspring older than cubs)
- **0** Non-production of surviving cubs inferred by absence of offspring in later years
- (gray) 2 No. cubs in a surviving litter inferred by observation of yearlings the following year
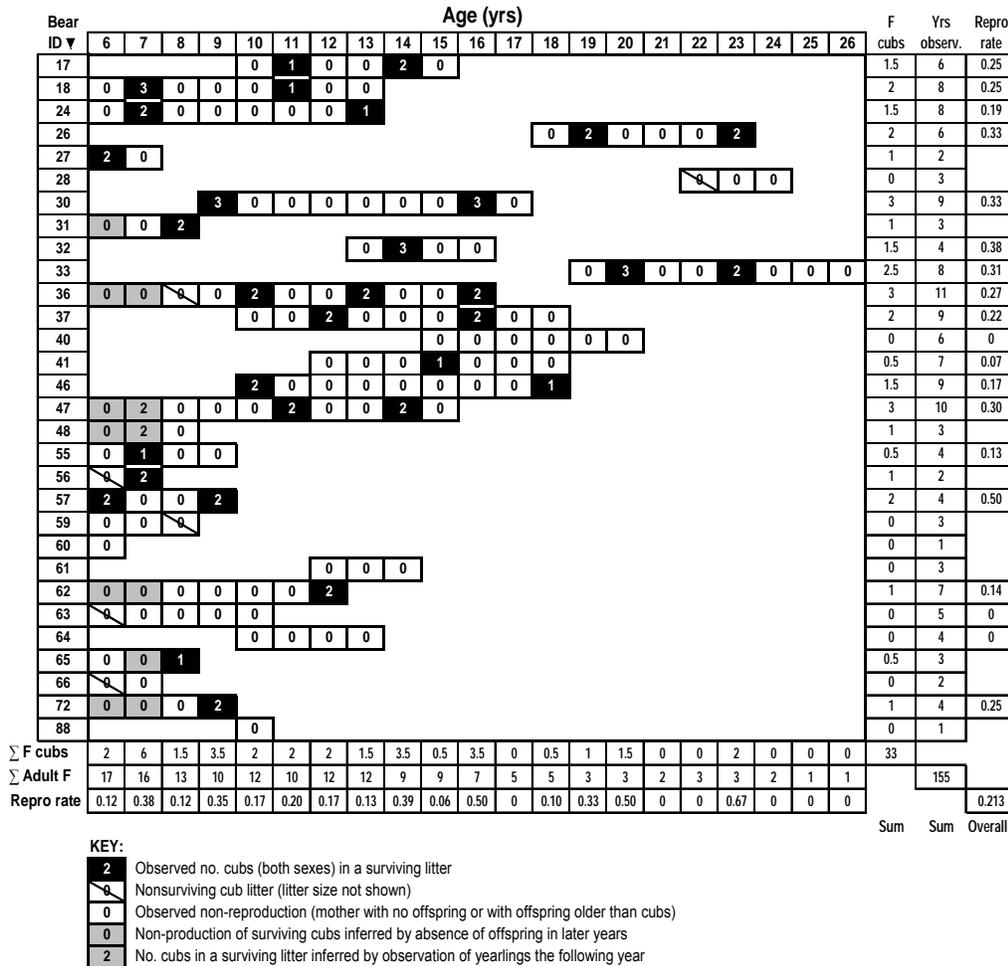
Figure 2. Reproductive records (considering only surviving litters) of radiomarked adult female grizzly bears in the Bow River Watershed, 1994–2002, aligned by age. Age-specific reproductive rates (Σ female cubs/ Σ adult females monitored; cub sex ratio assumed to be 1:1) are shown along the bottom, and individual reproductive rates (for bears that were monitored ≥4 years) are shown along the right side.

An average female bear in this population, which began producing cubs at 6.7 years old and lived to reproductive senescence, would give birth to 4.9 female cubs, of which 3.5 would survive to independence. However, most bears did not survive to the age of senescence. Based on matrix projections combining reproduction and survival, females produced, on average, only about 1.7 female cubs in their lifetime (R_o). The average time necessary to produce these cubs (generation time, T) was about 13.5 years (±0.5 years with varying assumptions regarding rates of reproduction and survival).

Population Growth

The range among all 8 estimates of λ was narrow (1.035–1.043), indicating that variations in assumptions, methodologies, and inclusion or exclusion of 1 female whose fate was uncertain did not

appreciably affect our assessment of population status. Jackknifed and bootstrapped confidence intervals were nearly identical. In all cases, 95% CIs for λ included 1.0 (0.99–1.09). However, 90% CIs did not overlap 1.0 when the 1 female with an uncertain fate was not considered a mortality (1.00–1.09). When this bear was censored at the time of its disappearance, 93% of bootstrapped resamplings yielded a λ that was not declining (≥1.0); when this bear was considered to have died, 90% of runs were not declining. Bootstrapping results indicated a 3–6% probability of estimated λ < 0.99, 9–13% probability of 0.99 ≤ λ ≤ 1.01 (fairly stable population), and 82–88% probability of λ > 1.01.
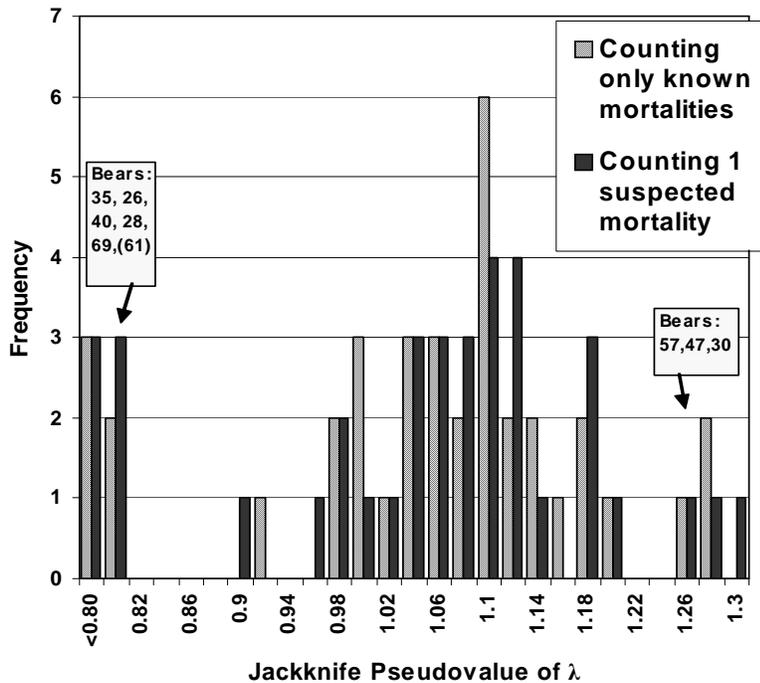
Figure 3. Distribution of jackknifed pseudovalues of λ derived from data on radiomarked female grizzly bears in the Bow River Watershed, 1994–2002. Each female's survival and reproductive record (considering only surviving litters) was deleted one at a time, and λ recalculated with a Leslie matrix. Each recalculated λ was multiplied by n-1 (n = 37 females) and subtracted from the full-sample estimate of λ multiplied by n to obtain pseudovalues ($\bar{x}$ = 1.04, 95% CI = 0.99–1.09). Individual bears in the tails of the distribution are identified (1 bear that was suspected of being killed is identified parenthetically).

Six bears in the sample of 37 females were responsible for stretching the confidence interval below 1.0 (Fig. 3). Logically, these were all bears that died, and in particular included the only 2 subadult female mortalities that we observed. The adults included 1 bear (#40) that from age 15 to 20 produced no cubs, 1 bear (#26) that lost a 2-cub litter over a period of 2 years, waited 2 more years to produce another litter, then died while raising that litter, and a 22-year-old (#28) that was the only multiparous female whose cub litter did not survive a full year (Fig. 2). Conversely, adults at the other end of the spectrum, that elevated the estimate of λ, included 2 bears (#30, 47) that successfully raised 6 cubs in 9 years with no mortalities, and 1 bear (#57) that gave birth at the minimum age of 6, successfully raised 2 cubs, and then gave birth to another 2 cubs 3 years after the first litter; this bear had the highest individual reproductive rate (Fig. 2).

The projected stable age distribution among females in this population included 12% cubs, 17% 1–2-year-olds, 19% subadults (3–5-year-olds), and 52% adults. The ratio of adult:subadult females in the projected population was 2.7:1. In our capture sample this ratio was 2.2:1. When males were added to the matrix they comprised 50% of dependent young (by definition), 43% of subadults, and only 23% of adults. The population growth rate was unaffected by the addition of males. However, if females had the same survivorship as males, the population would plummet (λ = 0.91–0.93).

Summed elasticities for female survival (0.92) far exceeded elasticities for reproduction (0.08, averaged among various scenarios). The elasticity for adult survival (0.46) was twice that of independent subadults (0.23) and dependent young (0.23). However, adult female survival actually varied much less across years than survival of younger-aged bears, and survival overall was considerably less variable from year to year than reproduction (Table 4). This variability reduces the precision of the mean matrix from which these elasticities were derived. We recalculated λ from matrices in which each parameter was separately reduced to its lower 95% confidence limit, while holding all others constant, and found that whereas adult survival

still had a large effect, annual variability in other vital rates had a greater effect on population growth than indicated by their relative elasticities (Table 4).

Table 4. Variation in vital rates and variation in population growth rates as a function of vital rates for grizzly bears in the Bow River Watershed, Alberta, 1994–2002. Elasticities (proportional change in λ in response to a proportional change in 1 of the vital rates) indicate a major influence of adult female survival. However, other parameters may be more variable, and thus have a larger effect on actual variation in λ than indicated by their elasticities.

	Estimate	CV[a] among years	95% CI[a]	Decline in λ at lower CL[b]	Elasticity
Reproductive rate					
All litters	0.24	62.4%	0.19–0.29	1.9%	8%
Surviving litters[c]	0.21	62.6%	0.17–0.26	1.8%	8%
Cub–yearling survival					
All litters	0.72	31.4%	0.55–0.91	2.1%	23%
Surviving litters[c]	0.81	31.2%	0.65–0.97	1.6%	23%
Subadult female survival	0.92	16.7%[d]	0.79–1.00	3.5%	23%
Adult female survival[e]	0.96	4.8%	0.92–1.00	2.5%	46%

[a] CVs and CIs shown on table include both process and sampling variation, but only process variation affects λ.
[b] Decline in estimate of population growth if this parameter is reduced to its lower confidence limit, while all other parameters remain fixed.
[c] Considering only litters in which ≥1 cub survived.
[d] High CV due to small sample size (only 2 of 9 years with survival <100%).
[e] Including only documented deaths (1 adult female with an uncertain fate was censored).

As a management guide, we calculated combinations of adult and subadult female survival rates that this population could withstand (i.e., combinations resulting in λ = 1.0). If adult and subadult survival rates were the same, then an overall female survival of 91% would maintain this population (Fig. 4). In our 9-year study, this survival target rate would have been met even if 1 more radiomarked female had died every other year. If these additional mortalities had occurred, however, we would have been much less assured of the status of this population, as CIs around λ would have widely-overlapped 1.0, even if the point estimate was ~1.0. Our estimated survival rates under the old management system indicate that the population would be declining (λ = 0.98, Fig. 4) had efforts to reduce grizzly bear mortality not been instituted.

DISCUSSION
Survival
Females in the BRW had high rates of survival. Excluding human-caused mortality, survival of females after leaving their mother was nearly 99%. This matches what has been reported for some populations of polar bears (*U. maritimus*), where radiotelemetry data yielded higher estimates than previously thought possible (Amstrup and Durner 1995). It might seem illogical that survival could really be this high. In a telemetry study, if 20 bears were tracked from maternal independence at age 3 to age 23, at which point they all died, the calculated survival rate would be only 95% (20 deaths/[20 · 20 bear-years] = 5% mortality). Obviously this case is unrealistic, as even in the absence of human-caused mortality some bears would die before age 23, thus reducing survival below 95%. However, it is important to consider that in most telemetry studies, including ours, bears are not followed to their death at old age. The estimated survival rate is thus the rate up to but not including deaths due to old age. This is exactly what is needed for use in estimating population growth from a Leslie matrix, where reproduction is truncated at the age of senescence, effectively eliminating

the old bears. Including mortality of post-senescent bears as part of an average rate for adult females would cause this estimate to be biased low, and thus under-rate the population's growth rate. In our study, a 24-year-old female that was killed by another bear may have suffered this fate in part because of her advanced age, but she was nonetheless younger than our presumed age of senescence and accordingly was counted in the estimate of adult survival.
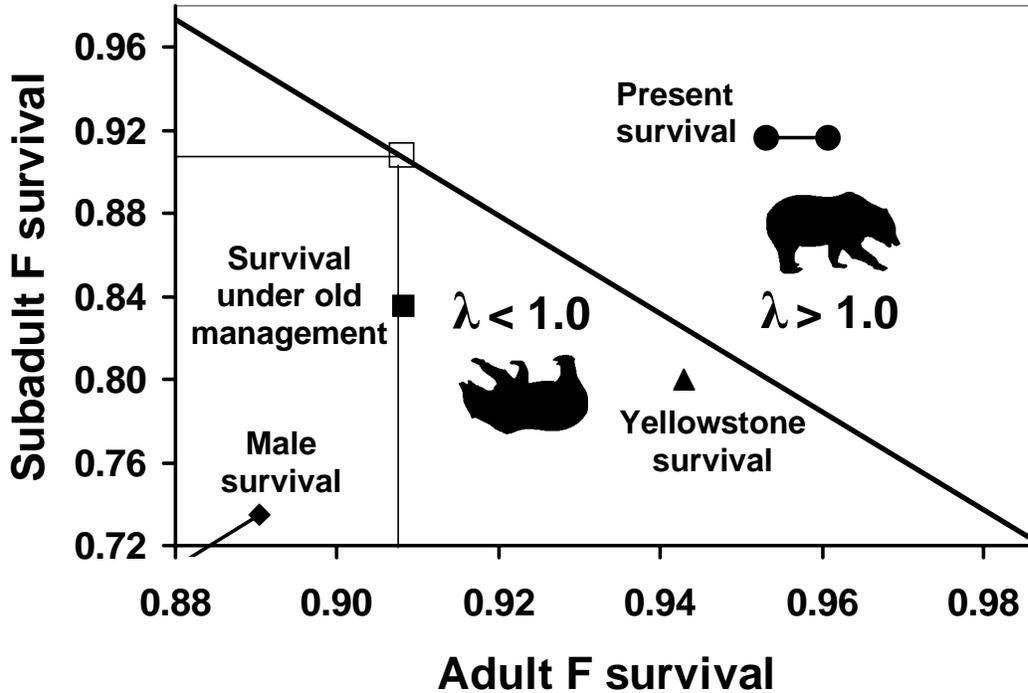

Figure 4. Combinations of adult and subadult female survival resulting in positive or negative population growth rates for grizzly bears in the Bow River Watershed. The diagonal line represents combinations yielding population stability, and the open square (□) is the situation where λ = 1.0 and adult and subadult survival are equal (0.91). X- and Y-intercepts represent survival excluding human-caused mortality (maximum limits). Labeled points show the presently observed situation (2 scenarios: ●), and 3 hypothetical situations: (■) survival rates under the previous, less protective management system in the BRW, (◆) survival rates of males applied to females (1 scenario is out of range of the graph), and (▲) survival rates of female grizzlies in Yellowstone combined with reproductive rates of bears in the BRW.

Another issue possibly affecting the estimation of survival is the loss of animals with low survival and retention of study animals with high survival, eventually leading to a biased sample (Zens and Peart 2003). The longer the study period, the more apt the sample is to become dominated by older and longer-lived individuals. If this occurred during our study, however, we should have noticed an increase in survival through time. This did not occur, probably in part because we continued to radiomark new bears of both sexes through the duration of the study.

Males had a lower rate of survival than females, due to higher mortality from human-related causes. Male home ranges averaged nearly 3x larger than those of females, and their risk of mortality was also about 3x greater, but home range size, independent of sex, did not explain an appreciable portion of the variation in bears' susceptibility to mortality.

Seemingly contrary to our findings, Benn and Herrero (2002) reported that females constituted 80% of human-caused mortalities in Banff and adjacent Yoho National Parks during 1985–98. However, their data were obtained from park records of deaths and translocations, not telemetry, so bears that left the parks and were killed outside would not have been included. Among our radiomarked sample, 90% of human-caused

male mortalities (9 of 10) occurred outside BNP, whereas only 60% of the females (3 of 5) that died of human-related causes were outside the park. This likely accounts for the difference between our results and those of Benn and Herrero (2002), and also explains our inability to discern differences in survival between what we considered park bears and non-park bears; indeed, 3 males that we classified as park bears were killed outside the park.

Habituation to humans is another factor often associated with increased risk of mortality (Meagher and Fowler 1989, Mattson et al. 1992, Pease and Mattson 1999). About twice the percentage of females (35%) as males (18%) in our radiomarked sample were considered human-habituated. These females were somewhat more prone to being killed or otherwise removed from the population than females that did not frequent areas of human activity. However, heightened mortality among habituated bears was apparently much greater in the past, before management authorities cleaned up food and garbage attractants and began making a concerted effort to keep human-habituated bears alive (Benn and Herrero 2002).

Reproduction

Reproductive rates of bears in our study were among the lowest reported for this species. To some extent this is due to improved (less biased) methodology for estimating reproductive parameters, but to a larger extent the contrast is real.

Of the parameters that relate to a female bear's productivity — age of first and last reproduction, litter size, and interval between litters — age of first reproduction appears to be most sensitive to local food conditions (Noyce and Garshelis 1994, Ferguson and McLoughlin 2000). Among interior populations of grizzly bears in North America, vegetational productivity (indexed by evapotranspiration) accounts for >90% of variation in age of first cub production (Ferguson and McLoughlin 2000). Our results, even based on the conventional (low-biased) estimator, suggest a slightly higher age of first reproduction (6.6 years) for this population compared to other interior populations at this latitude (5.5–6.1 years; McLellan 1994, Ferguson and McLoughlin 2000). Our estimated average age of first reproduction for surviving litters (8.4 years) was quite a bit higher than the age for all first litters, but this statistic has not routinely been reported in other studies so we cannot judge its comparability. McLoughlin et al. (2003) reported a similar average age of first production of a surviving litter (8.2 years; recalculated using our methodology) for grizzlies in the Canadian Arctic barren-grounds. An even older age of first successful reproduction (> 9 years) was observed in southwestern Alaska, but this was attributable to low survival of litters rather than delayed birthing (S.D. Kovach, U. S. Fish and Wildlife Service, personal communication).

The average interval between births in our study (4.4 years) was also greatly extended. Among only 11 bears in our study for which we observed at least 2 litters, 1 retained a litter for 4 years and had a known inter-litter interval of 7 years, and another raised a litter for 5 years and produced a second litter after 8 years (birthing in the first and last years of the study); these litter intervals equal the longest reported for this species. Craighead et al. (1995) observed 2 open-ended intervals of >7 years among 30 female grizzlies monitored over 11 years in Yellowstone National Park, Wyoming. Others (P. L. Clarkson and I. S. Liepins. 1993. Female productivity and cub survival of grizzly bears in the Anderson and Horton Rivers area NWT, 1987–92. Inuvialuit Wildlife Studies Program Report, Northwest Territories Department of Renewable Resources, Inuvik, Northwest Territories, Canada; Sellers and Aumiller 1994; R. A. Sellers, S. Miller, T. Smith, and R. Potts. 1999. Population dynamics of a naturally regulated brown bear population on the coast of Katmai National Park and Preserve. Final Resource Report NPS/AR/NRTR–99/36, National Park Service and Alaska Department of Fish and Game, Anchorage, Alaska, USA1999; S. D. Kovach, personal communication) observed notably long intervals between production of surviving (weaned) litters (Table 5), but these were due to low survival of litters. In our study all nonsurviving litters were either the bear's first or last litter; hence the interval was approximately the same whether counting all litters or just surviving litters.

Mean cub litter size in grizzly bear populations has been reported to range from 1.6 to 2.5 (summarized by: LeFranc et al. 1987; Ballard et al. 1993; McLellan 1994; P. I. Ross. 2002. Update COSEWIC status report on the grizzly bear *Ursus arctos* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada). The mean litter size observed in our study (1.8 cubs) is near the low end

of this range. Relationships between grizzly bear litter size and environmental productivity are less definitive than with age of first reproduction and litter interval, but still seem to show a trend (Stringham 1985).

The combination of long inter-litter intervals and small litter sizes yielded a low reproductive rate among adult females. Considering also the effects of delayed age of first birthing, bears in this population had the lowest potential lifetime cub production of any population yet studied. Given equal survival, adult females in other populations at this latitude or even much further north, would produce at least 50% more cubs over their lifetime (Table 5). It would appear that cub production in the BRW is limited by nutrition; however, we were unable to identify any habitat features within home ranges that explained variation in individual reproductive rates. Similarly, Aune et al. (1994) found that variation in reproductive rates of grizzly bears within their Montana study area did not conform to expectations based on their subjective assessment of habitat quality.

Wielgus and Bunnell (2000), who studied grizzly bears in a portion of our study area (Kananaskis) during the early 1980s, postulated that low reproduction was caused by a high turnover of adult males (from hunting), resulting in younger immigrant males displacing females from preferred feeding areas. That explanation was not upheld by our study. Hunting in this area has ceased, so although subadult male turnover (mortality) was fairly high, adult male turnover was low, yet the reproductive rate remained low (Table 1). Notably, although the reproductive rate that we observed was similar to that reported by Wielgus and Bunnell (1994a), the low rate in our study was due to extended litter intervals and somewhat delayed ages of first reproduction, whereas in their study the low rate was attributable to an unusually small litter size (Table 5). We cannot discount the possibility that males, in general, displaced females from better feeding areas (Wielgus and Bunnell 1994b), a situation that occurs even in unhunted populations of many species of bears (Garshelis and Pelton 1981, Derocher and Stirling, 1990, Joshi et al. 1995, Hwang 2003), but we think it is unlikely that males were ultimately responsible for the low productivity of females. The body condition index (Cattet et al. 2002) of BRW males, but not females, was lower than that of a more productive nearby grizzly population (Jasper National Park), although both sexes in BRW showed depressed levels of luteinizing hormone, which may have disrupted reproductive functions (M. R. L. Cattet, N. Caulkett, M. Gibeau, S. Herrero, J. Bahr, J. Van Cleef, and G. Stenhouse. 2003. Comparison of select health data between Eastern Slopes (ESGBP) and the Foothills Model Forest Grizzly Bear Projects (FMFGBP). Pages 13-16 in M. L. Gibeau and S. Stevens, editors. Grizzly bear monitoring in the Bow River watershed: a progress report for 2002. Parks Canada, Banff National Park, Alberta, Canada). We suggest that the low reproductive rate was most likely a result of limited nutrition, due to a low contribution of meat in the diet (Hamer and Herrero 1987; L. Felicetti, C. T. Robbins, S. Herrero, and M. Pinto, unpublished isotopic analysis of hair) — meat being directly linked to reproductive output in grizzly bears (Hilderbrand et al. 1999) — and also restrictions on where bears could feed without being disturbed by humans (Gibeau et al. 2001).

Whereas productivity among BRW females was low, survival of their young through the period of maternal dependency was at or above average compared to other areas. Cub survival was near the median rate (~75%) among studies from elsewhere in North America (Garshelis 2004), and was considerably higher (89%) when nonsurviving first litters were excluded. Yearlings also had a relatively high rate of survival (Table 5), as did older dependent young (none of which died). Although the lengthy maternal care exhibited by mothers in our study (averaging 3.4 years) diminished the frequency of births, the increased survival of offspring stemming from increased maternal care appeared to be an adaptive trade-off. Some other grizzly bear populations have employed the alternate strategy of higher reproduction but consequently lower survival of dependent young (e.g., Nunavut, Susitna, Table 5). These contrasting population strategies may be linked to differing sources of mortality of dependent young, which are, as yet, poorly understood.

Population Growth

Our combined estimates of survival and reproduction indicate that the grizzly bear population in the BRW has been growing by about 4% per year. This was an unexpected finding given that definitive population growth (λ lower CL >1) has not been observed in any other grizzly population with a reproductive rate <0.3 (Table 5). Confidence intervals around our estimate of λ allowed for the possibility that the population was actually declining. However, the width of these CIs was exaggerated by the inclusion of sampling variation in all of our parameter estimates, whereas only process (temporal, spatial, individual) variation actually affects population dynamics (Gould and Nichols 1998, White 2000).

Table 5. Demographic parameters[a] used to estimate population growth rate (λ) in studies of grizzly bears across North America, ordered by reproductive output (except that the 2 Kananaskis studies are placed together).

Area [b]	Age 1st birthing		Age last birthing		Litter size	Litter interval	Repro rate[d]	Max. lifetime repro[e]	Survival				λ	
	min	$\bar{x}$	observed	assumed[c]					Cubs	Yrlings	Sub F	Ad F	Point est.	95% CI
Flathead, BC, Can.	5	6.4		20	2.3	2.8	0.42	8.7	87%	94%	93%	95%	1.09	1.03–1.14
Nunavut–NWT, Can.	5	8.1	26	25	2.2	2.8	0.41	7.7	74%	68%	~83%	98%	1.03	1.01–1.06
Susitna River, AK, USA	4	5.6	26	26	2.1	2.8	0.36	7.7	64%	88%	86%	92%	1.02	
Yellowstone, USA	4	5.6	25	20	2.2	2.8	0.35	7.5	84%	84%	80%	94%	1.05	0.97–1.12
Kuskokwim Mts, AK, USA	4	7.2	26	28	2.0	2.6	0.30	6.0	55%	78%	87%	94%		1.00–1.02
Selkirk Mts, USA–Can.	6	6.5		27	2.2	3.5	0.29	5.9	88%	78%	90%	94%	1.02	0.92–1.10
Cabinet–Yaak, USA	6	6.6		27	2.1	3.0	0.29	5.9	68%	88%	77%	93%	0.96	0.84–1.06
Swan Mts., MT, USA	4	6.0	23	25	1.6	3.0	0.26	5.5	79%	90%	83%	90%	0.98	0.88–1.05
Katmai, AK, USA	6	7.2	23		2.1	5.8[f]	0.25	5.0	34%	79%	100%	91%	0.98	
Kananaskis, AB, Can.	4	5.0[g]		21	1.4	3.0	0.23	5.1	~78%	~78%	~89-93%	93%		0.99–1.01
Banff-Kanan., AB, Can.[h]	6	6.7	23	26	1.8	4.4	0.24	4.9	79%	91%	92%	95-96%	1.04	0.99–1.09

[a] Blank cells indicate no information presented by authors and value not calculable from their report; ~ symbol indicates that study had insufficient data to estimate value directly.

[b] Sources of data: Flathead (Hovey and McLellan 1996), Nunavut–NWT (McLoughlin et al. 2003, superseding Case and Buckland 1998), Susitna River (Miller 1997*a,b*; S.D. Miller, National Wildlife Federation, personal communication), Yellowstone (L. L. Eberhardt. 1995. Population trend estimates from reproductive and survival data. Pages 13–19 *in* R. R. Knight and D. M. Blanchard, editors. Yellowstone grizzly bear investigations; annual report of the Interagency Study Team 1994. National Biological Service, Bozeman, Montana, USA), Kuskokwim Mountains (S. D. Kovach, U.S. Fish and Wildlife Service, personal communication), Selkirk Mountains (Wakkinen and Kasworm 2004, superseding Wielgus et al. 1994), Cabinet–Yaak (Wakkinen and Kasworm 2004), Swan Mountains (Mace and Waller 1998), Katmai (R. A. Sellers, S. Miller, T. Smith, and R. Potts. 1999. Population dynamics of a naturally regulated brown bear population on the coast of Katmai National Park and Preserve. Final Resource Report NPS/AR/NRTR–99/36, National Park Service and Alaska Department of Fish and Game, Anchorage, Alaska, USA; R. A. Sellers, Alaska Department Fish and Game, personal communication), Kananaskis (Wielgus and Bunnell 1994*a*), Banff-Kananaskis (this study).

[c] Age of last birthing assumed in Leslie matrix or Lotka equation, used to calculate λ.

[d] Reproductive rate (female cubs born per adult female), often estimated from (mean litter size/2)/mean litter interval.

[e] Potential number of female cubs produced if a female lived until reproductive senescence, assumed to be 27 years in all cases (Schwartz et al. 2003); calculated as: (27 – mean age of first reproduction) · (reproductive rate).

[f] Intervals between weanings, not births; long intervals were due to frequent whole litter loss.

[g] Value recalculated; authors inappropriately added a half year to all ages.

[h] This study: reproductive data include nonsurviving litters, to be consistent with most other studies. However, estimates of age of first reproduction, litter interval, and reproductive rate are derived from methods that generally differ from other studies.

If the population had been growing at 4% per year, then it would have increased nearly 40% during the course of our study. Such an increase was not noticed. Unduplicated counts of females with cubs, a potential index of population size (Knight et al. 1995) showed no trend (M. L. Gibeau and S. Stevens. 2003. Grizzly bear monitoring in the Bow River watershed: a progress report for 2002. Parks Canada, Banff National Park, Alberta, Canada). Either this index was not sensitive enough to detect a trend, or our estimate of population growth was incorrect.

Population growth in the BRW would be less than we estimated if many of the added bears emigrated. Our estimate assumed the population to be geographically closed. Although we recognized this area as not being closed, we did not witness emigration of radiomarked females, and inasmuch as our estimate of population growth was derived only from females, male emigration would be inconsequential. Other studies of even more rapidly increasing grizzly-brown bear populations also observed limited emigration of females (Swenson et al. 1998, McLellan and Hovey 2001)

Stochasticity and density dependent factors, which were not included in our analysis, would depress the population growth rate below what we estimated (Benton and Grant 1999). An over-estimation of the age of reproductive senescence also would have inflated our estimate of λ. Others have generally assumed, more by convention than from empirical data, that females do not produce beyond 20–25 years of age (Table 5). We chose 26 as the last potential year of birthing, even though the oldest age of birthing in our study was only 23 years old (rationale explained earlier). Had we used 23 years instead, we would have obtained population growth rate estimates averaging 3.5%.

Variability among bears and non-representative sampling of this variability also could have biased our estimate of population growth. For example, under-representation of human-habituated bears (having lower survival) in the radiomarked sample would cause an over-estimate of λ (Pease and Mattson 1999). However, we considered more than a third of our female sample to be human-habituated, and we still could barely discern a difference in survival between these bears and more wary bears because so few females died. Also, unlike the Yellowstone situation, where year-to-year fluctuations in a single food item had large effects on survival (Mattson et al. 1992), we observed relatively constant survival among females during this 9-year study.

We did observe significant year-to-year variation in reproduction, as well as an indication of possible differences in age-specific reproductive rates. This variability could result in an unstable age distribution, a violation of an assumption of the Leslie matrix. However, slight deviations from a stable age structure are not necessarily problematic. The overall λ is just the weighted average of the growth rates of all the separate age classes, some strong, some weak (Sibly and Smith 1998). The real danger would be in deriving λ from vital rates that were changing directionally through time, which was not the case in our study. Moreover, we obtained nearly the same estimate of λ whether or not age-specific reproductive rates were included in the Leslie matrix. This finding coincides with that of Gilbert and Udevitz (1997), who modeled population growth for species with multiple-year reproductive cycles, including bears. In general, for many long-lived species, with undoubted yearly fluctuations in reproduction and/or survival (and hence age structures), studies have shown strong concordance between estimates of population growth derived from vital rates and from trend data (periodic counts or population estimates; Eberhardt 2002, Sandercock and Beissinger 2002).

Sensitivities and elasticities of the Leslie matrix transition elements indicated that the growth rate of the BRW population would be most affected by changes in adult survival. This finding has previously been reported for both hunted and unhunted grizzly bear populations (Wielgus et al. 2001). For long-lived animals in general, elasticities for adult survival tend to be highest (because adulthood spans such a long period of time), even though, as in our study (Table 4), juvenile survival and reproduction are usually more variable (Gaillard et al. 1998, Heppell et al. 2000, Sæther and Bakke 2000).

MANAGEMENT IMPLICATIONS

Our study yielded 2 especially noteworthy implications for grizzly bear management in the BRW. First, we found that this population is at the low extreme in terms of grizzly bear reproduction, so the potential for population growth is limited. Therefore, an attentive management program to limit human-caused mortalities is necessary. Second, we found that survival rates during our study, which were higher than under the

previous management system, seemed adequate to sustain this population; that is, the grizzly bear management program currently in place seems to be accomplishing its goal.

To assess whether managers are continuing to achieve their goal of sustaining a source (growing) population of grizzly bears, they could monitor survival rates using a sample of radiomarked females similar to ours. A survival rate of 91% should prevent population decline, although this target would be risky, as it does not consider either environmental stochasticity or sampling error. A safer goal would be to maintain the same rate of female survival that we actually observed in this study, overall about 95%, given that the lower 95% CL on this estimate was 91% (Table 1).

Survival also could be monitored without radiomarking, just by tallying known dead bears. Benn and Herrero (2002) did this while we conducted a companion telemetry study. They documented a decline in mortality, commensurate with dramatically improved human food and garbage management and more protective management policies. Using their data as a baseline representing positive population growth, management authorities could strive to ensure that total mortality did not increase beyond this. Radio-telemetry, though, would be a more reliable means of obtaining mortality data.

Whereas survival of grizzlies would likely decline under a more lax management program, increasing survival of grizzlies in the BRW beyond what has already been achieved is probably not feasible. Even in the high-profile grizzly bear population of Yellowstone National Park, USA, management efforts that successfully reduced human-caused mortality and enabled the reversal of a downward population trend (Eberhardt and Knight 1996) resulted in survival rates lower than what is necessary to sustain the population in the BRW (Table 5, Fig. 4).

Human-caused mortalities will likely increase in the future as the human population near the BRW continues to grow. The population of Calgary, the main urban center near the study area, increased by over 15% during 1996–2001, which, for that period, was the highest growth rate for a large urban area in Canada. This growing population places great demands for recreation, resource harvest, settlement expansion, transportation corridors, and other uses of the BRW landscape.

Upholding the level of survivorship necessary to sustain this population requires not only great effort and expense, but also sacrifices in terms of human use of the area. This is bound to create some animosity among potential users and raise questions about the need for ever-increasing measures to further protect grizzly bears (B. Cooper, J. Hayes, and S. LeRoy. 2002. Science fiction or science fact? The grizzly biology behind Parks Canada management models. Fraser Institute Critical Issues Bulletin, Vancouver, British Columbia, Canada). Those with that view may interpret our research results as evidence that the population is now growing and out of danger, and that accordingly, fewer restrictions on human development and activities are warranted.

We stress, however, that our results include many uncertainties, both in assessing short-term population trend, and, even more so, in forecasting future trends. Whereas our study was long enough to obtain data sufficient to produce adequate estimates of demographic parameters, it was but a snapshot in terms of grizzly bear population dynamics. For a small population like this, vulnerable to the impacts of varying human behaviors and environmental events, it seems only sensible to err on the side of prudence. So far, however, it appears that efforts designed to safeguard this population are working.

ACKNOWLEDGMENTS

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5.2 GRIZZLY BEAR DEMOGRAPHICS IN AND AROUND BANFF NATIONAL PARK AND KANANASKIS COUNTRY – POSTSCRIPT FOR 2003-2004

David Garshelis, Michael Gibeau, and Stephen Herrero

Following 9 years of intensive study (1994–2002) of grizzly bears in Banff National Park and Kananaskis Country, mortality monitoring was continued for another 2 years. A sample of 18 radiocollared females and 9 males were tracked from the ground during 2003–2004, including 3 females and 4 males that were caught in 2003. No new bears were added to the sample in 2004.

Two females and 3 males died in 2003 and 4 females and 2 males died in 2004. Four (36%) of these (2 males, 2 females) were natural mortalities, 3 caused by other bears and 1 by wolves. The 7 human-related losses (4 females, 3 males) were the result of collisions with a vehicle on the highway (n = 2), translocations due to nuisance activity (n = 3) or being shot (n = 2). Some collared bears were lost track of either because their collar dropped off or because they lived in remote areas where ground monitoring was not feasible. By the end of 2004, only 9 females and 1 male remained in the monitored sample.

Estimated survival for females (all ages pooled) based on these data was 88% (95%CI 74–100%) in 2003 and 71% (CI 47–99%) in 2004. Although confidence intervals on these estimates (based on the cumulative hazard; Link 1984) were wide, it appeared that these rates were well below the mean and confidence intervals of the previous 9 years (95% CI 91–99%, yearly range 93–100%). They were also below the minimal rate of survival (91%) necessary to sustain this population (i.e., to achieve $\lambda = 1$), given previous reproductive output.

Male survival, although not relevant to population growth rate, was also lower than normal in both these years (65% in 2003; 40% in 2004; 1994–2002 $\bar{x}$ = 81%, 95% CI 71–91%). Two peculiarities, though, detract from the reliability of the male estimates. First, one of the collared males that was killed by another bear had been orphaned as a cub (and was collared specifically as a result of this); had this not occurred, this bear likely would have been under the protection of its mother in May 2003, when it was killed at age 2. Excluding the data on this individual, estimated male survival was 77% in 2003 (within the previous CI). Second, the low estimate for 2004 was at least partially the result of small sample size: by June only 2 males were being monitored, 1 of which died.

The low rate of survival in these 2 years, at least for females, prompted this postscript to our paper. In the first 9 years, only 3 bears died of natural causes, whereas in these last 2 years, 4 natural mortalities occurred. Both females that died naturally (1 killed by a bear, 1 by wolves) were advanced in age (19 and 20 years old); although they were younger than the natural maximum lifespan for a grizzly bear (25–30+ years), they were likely more susceptible to being preyed upon than when in their prime. These bears had been radiocollared since 1994–95, so with each passing year of monitoring, they became increasingly likely to die. This potentially confounding problem of bears aging was not an issue during the 9-year study when new bears were added to the sample each year.

A second factor that likely affected survival was a widespread shortage of natural foods in 2004, which could have prompted more intra-specific strife, especially as bears competed for available foods. Low abundance of natural foods also may have prompted more bears to approach human food sources, where they were more likely to be shot, killed crossing a road, or translocated due to recurring nuisance activity. Three bears were translocated in these last 2 years, equaling the number translocated in the previous 9 years. Possibly, managers, who strove to keep these bears alive and in the population during the course of the study, felt less obliged to do so after the study officially ceased in 2002, and elected to translocate, rather than continue to deal with bears that were repeatedly involved in conflicts with humans.

Results from these last 2 years of monitoring reemphasize two important points discussed in our previous paper: (1) the effects of stochastic events (and possibly increased density-dependent effects) on grizzly bear demographics, and (2) the importance of continued monitoring for a population like this, where slight changes in bear or human behavior that influence grizzly bear mortality can tilt population trend from positive to negative.

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5.3 GRIZZLY BEAR POPULATION DENSITY ESTIMATES WITHIN THE CRE

Stephen Herrero

In 1997, as part of the ESGBP, we did a low-budget attempt to derive a DNA-based capture/recapture estimate of grizzly bear abundance and density for the Bow River Watershed portion of the ESGBP study area (Sherry 1996, Proctor 1998). We used radio-telemetry locations to help correct for lack of closure for the study area. Despite this, the best estimate of density, 1.2/100 km², had a wide confidence interval (90% CI: 0.7 – 2.7/100 km²) (Proctor 1998).

Two prior studies, each using a similar sample of radio-collared grizzly bears, captured 1980–1984, generated population density estimates for grizzly bears living in and near Kananaskis Country. Carr (1989) used the Chapman-Robson mark-recapture technique to estimate the number of male grizzly bears. He assumed a sex ratio of 1:1 to estimate the number of females. Wielgus and Bunnell (1994) questioned the validity of this assumption and reported that for mostly the same sample from the same area the sex ratio was skewed towards males. As well Wielgus and Bunnell found immigration of males. This was taken as evidence for lack of closure of the population. Carr (1989) assumed he was sampling from a closed population. Wielgus and Bunnell (1994) estimated the mean annual density of bears by determining the mean annual number of bears present in the 97.5% multi-annual, composite home range of females. They suggested that all bears were accounted for in that 868 km² area but present no evidence to substantiate this claim. Both studies had methodological uncertainties and small samples. Neither presented confidence intervals around their point estimates of density. The Carr (1989) density estimate was 1.2 bears/100 km². The Wielgus and Bunnell (1994) estimate was 1.6 bears/100 km².

Despite methodological uncertainties, the reasonable convergence of the Carr (1989), Wielgus and Bunnell (1994), and Proctor (1998) population density estimates is worth noting despite their lack of precision and perhaps even validity. This convergence suggests very cautious use of the range of these 3 estimates, 1.2 – 1.6/100 km², not forgetting the large confidence intervals of the only study calculating CIs (Proctor 1998). In 2004, Stenhouse and others (Biologist, Foothills Model Forest, Hinton, Alberta, personal communication) conducted a DNA capture/recapture study in a north eastern portion of the CRE in Alberta. This study design improved substantially on that of the ESGBP (Proctor 1998). Results are not yet available but they should be more precise.

Even with improved research design there will remain challenges with extrapolating from one area to another regarding population density estimates and related point estimates of population abundance. One problem that will not easily be addressed is that extrapolation beyond a specific study area is only valid for areas of similar habitat productivity and grizzly bear demographics. For this and other reasons the ESGBP focused its efforts to understand population characteristics on demographic, long-term study of survival and reproduction of a large, radiomarked, random sample of grizzly bear cohorts in the Bow River Watershed (Garshelis et al. 2005). This has yielded precision and understanding regarding vital rates and their influence on population growth but has not allowed for a population density estimate or a point estimate of abundance.

A grizzly bear population density estimate also exists for the northwest portion of the CRE in British Columbia. DNA capture/recapture methods were used (Apps et al. 2004). Rigorous design and large sample sizes produced a population density estimate of 2.2 (95% CI 1.5 – 4.3)/100 km². Higher population density in this western slope of the Rockies area is predictable given more moisture and greater vegetation productivity. The higher west slope versus east slope density is paralleled by smaller home ranges for bears in the west slope portion of the CRE (Chapter 9, this report).

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5.4 THE EASTERN SLOPES GRIZZLY BEAR PROJECT'S POPULATION VIABILITY ASSESSMENT FOR THE CENTRAL ROCKIES ECOSYSTEM

Stephen Herrero

ESGBP demographic analysis documented the dynamics of births, deaths and population growth for a random sample of different age and sex classes of 71 grizzly bears found in the Bow River watershed, 1994–2002 (Garshelis et al. 2005). This allowed for an assessment of demographic parameters for this population during this time period. It identified demographic variables that had the most influence on population dynamics. The demographic study was not intended to project future potential grizzly bear population status, another conservation management need. A Population Viability Assessment (PVA) forecasts extinction risk or persistence for a species at risk over time (Boyce 1992). This entails the use of models. No matter how much data one has regarding a current population, assumptions must be made regarding its' future.

"Even though we often have insufficient data to perform PVA with statistical rigour, the model can be useful for framing our understanding of the principal processes that shape the species' dynamics" (Boyce 1995). Early PVAs for grizzly bears incorporated demographic and genetic stochasticity but did not incorporate the possible effects of habitat change (Schaffer 1978). However, the close relationship between habitat and population condition is fundamental. "…Progress towards species conservation goals should be measured with consideration of habitat area, quality, and associated spatial relationships" (Roloff and Haufler 1997). All species depend upon their habitat for survival. PVAs therefore must incorporate habitat to be comprehensive. Indeed recent users of PVA have argued not only for the incorporation of habitat within PVAs, but also for its use as a supporting tool for ranking management scenarios, rather than formal estimations of extinction risk (Possingham et al. 2002).

Rapid and extensive changes have occurred regarding grizzly bear habitat in the Central Rockies Ecosystem (CRE) (Gibeau 1998, Gibeau et al. 2001, Chapter 13, this report). This has resulted in little secure grizzly bear habitat. Habitat is secure in areas where research suggests adult female grizzly bears can meet their daily needs with a low probability of encountering a person (Mattson 1993, Gibeau et al. 2001). Grizzly bears in the CRE live in one of the most developed, least secure, landscapes in North America where the species survives (Gibeau 2000, Herrero et al. 2000).

Because of the extent of human activity and development in the CRE and the potential effects on grizzly bears, the ESGBP in 1999 undertook a PVA incorporating habitat considerations (Herrero et al. 2000). This was done in conjunction with the Conservation Biology Specialist Group (CBSG) of the International Union for the Conservation of Nature (IUCN). The initial work on the PVA was carried out in a retreat context over a 4 day period that brought together 87 people, including local researchers, other scientists (including expert research biologists and modelers), conservation and wildlife officers, land use planners, conservationists and business stakeholders. The PVA report is the only attempt by the ESGBP to project future conditions for grizzly bears at the scale of the entire CRE (about 40,000 km²) (Herrero et al. 2000).

The PVA model used was Vortex. The model identified 4 sub-regions in the CRE with the Trans-Canada Highway and the Rocky Mountains being unit boundaries internal in the CRE. Vortex allowed for different estimates of birth and death rates within each sub-region. CRE grizzly bears were assumed to be part of an open population. Therefore estimates of immigration and emigration were incorporated. Habitat quality and degree of human use and development were also incorporated into the model. Habitat-based models of grizzly bear probability of death were based on 2 things. First, most independent grizzly bears in the CRE die because humans kill them (Benn 1998). Second, human-caused deaths will occur at a rate governed by the frequency of encounters between humans and bears and the likelihood that a human will kill a bear during a given encounter (i.e. the potential lethality of contact) (Mattson et al. 1996). Probability of lethal contact is affected by policies of administrative jurisdiction, the most obvious being whether grizzly bear hunting occurs or not. Predicted variation in grizzly bear death rates were incorporated into habitat-based models derived from maps of jurisdictional boundaries, human facilities, roads and trails, human populations, and grizzly bear habitat productivity. The population model Vortex was used to predict the

probability of population decline or increase related to current levels. This was done by developing a series of stochastic simulation models of grizzly bear population viability. Probability of population decline or increase was chosen because all three major land managers in the CRE: Canada, Alberta, and British Columbia share the goal of having a non-declining grizzly bear population in the CRE.

Risk assessment projections depended most heavily on 2 demographic parameters: the percentage of adult females breeding and the rate of adult female mortality. Percentage of females breeding is influenced by age of first reproduction, senescence and interlitter interval. After the PVA was completed, subsequent demographic analysis of grizzly bears trapped in the Bow River watershed of Alberta (which is about one-fourth of the CRE) identified that these bears had the longest interlitter interval, latest age of first successful reproduction and lowest total reproductive output for any grizzly bear population studied in North America (Garshelis et al. 2005). Reproductive output is not likely to change very much since it is set by habitat productivity (Ferguson and McLoughlin 2000; also see Chapter 8, this report). Therefore, the bear population and its human managers must live with low reproductive output, at least in the Alberta portion of the CRE, and the knowledge that this significantly limits population resilience (Weaver et al. 1996). Adult female death rate, the other major variable influencing reproductive output, is more labile. The PVA modeling showed that a significant increase in the human population and related development would be predicted to cause further decrease in habitat security, increased contact between humans and female grizzly bears, an increased female grizzly bear mortality rate, and a related population decline (also see Chapter 13, this report).

The PVA workshop concluded that the impacts of humans on grizzly bear habitat and mortality must be reduced even while the numbers of humans in the region increase. It is unlikely that the number of humans coming into the area will decline dramatically. Therefore their impact on sensitive species such as grizzly bears will need to be addressed to prevent population decline. To do this the workshop recommended grizzly bear habitat restoration approaching 2% annually. Restoration would involve managing access and relocating human activities and facilities to less productive habitat to attain high survival rates for female grizzly bears. If this challenging task is not accomplished, and mortality rates for adult females increase, then population declines are inevitable. The workshop group recognized that there had to be a coordinated, joint management response from Alberta, British Columbia and Canada to manage the grizzly bear population and its habitat as a unit.

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