The Journal of Wildlife Management 9999:1–10; 2011; DOI: 10.1002/jwmg.250

Research Article

Grizzly Bear Population Vital Rates and Trend in the Northern Continental Divide Ecosystem, Montana

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ABSTRACT We estimated grizzly bear (*Ursus arctos*) population vital rates and trend for the Northern Continental Divide Ecosystem (NCDE), Montana, between 2004 and 2009 by following radio-collared females and observing their fate and reproductive performance. Our estimates of dependent cub and yearling survival were 0.612 (95% CI = 0.300–0.818) and 0.682 (95% CI = 0.258–0.898). Our estimates of subadult and adult female survival were 0.852 (95% CI = 0.628–0.951) and 0.952 (95% CI = 0.892–0.980). From visual observations, we estimated a mean litter size of 2.00 cubs/litter. Accounting for cub mortality prior to the first observations of litters in spring, our adjusted mean litter size was 2.27 cubs/litter. We estimated the probabilities of females transitioning from one reproductive state to another between years. Using the stable state probability of 0.322 (95% CI = 0.262–0.382) for females with cub litters, our adjusted fecundity estimate (m_x) was 0.367 (95% CI = 0.273–0.461). Using our derived rates, we estimated that the population grew at a mean annual rate of approximately 3% ($\lambda = 1.0306$, 95% CI = 0.928–1.102), and 71.5% of 10,000 Monte Carlo simulations produced estimates of $\lambda > 1.0$. Our results indicate an increasing population trend of grizzly bears in the NCDE. Coupled with concurrent studies of population size, we estimate that over 1,000 grizzly bears reside in and adjacent to this recovery area. We suggest that monitoring of population trend and other vital rates using radioed females be continued. © 2011 The Wildlife Society.

KEY WORDS grizzly bear, lambda, Montana, mortality, population trend, reproduction, survival, *Ursus arctos*.

The grizzly bear (*Ursus arctos*) occupies wilderness and non-wilderness habitats in the Northern Continental Divide Ecosystem (NCDE) of western Montana, USA. In 1975, this species was listed in the United States as Threatened under the Endangered Species Act because of threats to habitat and populations. At that time, there was limited information on the ecological requirements of the species and its population status. The NCDE supports the largest population of 6 designated recovery areas for the species (U.S. Fish and Wildlife Service 1993) in the lower 48 states and is contiguous with populations to the north in Canada.

Knowledge of population size and trend is useful to develop appropriate management programs for grizzly bears and to judge success of the recovery effort. In the Greater

Received: 9 November 2010; Accepted: 21 April 2011

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Yellowstone recovery area, population size was estimated from annual sightings and resightings of females with cubs (Knight et al. 1995, Keating et al. 2002, Harris et al. 2007). A population estimate for the NCDE, using grizzly bear hair collected at hair traps (Woods et al. 1999), was conducted in 2004. From this study, Kendall et al. (2009) estimated the population size was 765 individuals (95% CI = 715–831). Using similar methods, MacHutchon et al. (2008) estimated there were 228 (95% CI = 151–314) grizzly bears immediately to the north in Canada, in an area demographically connected to the NCDE population.

Concurrent with the 2004 study of population size in the NCDE (Kendall et al. 2009), an interagency team was established by state, federal, and tribal officials to estimate the trend of this population (Mace 2005). The primary objective was to monitor the survival and reproductive rates of a representative sample of radio-collared female grizzly bears from which population trend could be estimated. We report here on vital rates, and population trend of grizzly bears in the NCDE.

STUDY AREA

We studied grizzly bears in the NCDE of western Montana and into the Canadian provinces of British Columbia and Alberta. Our primary emphasis was within the 23,136 km^2 federal recovery zone in the United States (Fig. 1), although bears traveled beyond this zone. We also captured and monitored bears up to 16 km north of the United States into Canada, which enlarged the study area to approximately 24,000 km^2. There were 2 national parks in the study area: Glacier National Park in Montana (4,081 km^2) and Waterton Lakes National Park (505 km^2) in Alberta, Canada. Portions of the Blackfeet Indian Reservation and the Confederated Salish and Kootenai Reservation occurred within our study area. Notable roadless regions outside the national parks included the Bob Marshall, Great Bear, Scapegoat, and Mission Mountain federal wilderness areas in the US. Non-wilderness areas of the NCDE were characterized by multiple-use lands under public, state, corporate, and tribal ownership. Approximately 17% of the NCDE was private land.

The study area consisted of rugged mountain topography shaped by glaciation. West of the Continental Divide, lower elevation habitats were dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), subalpine fir (*Pinus albicaulis*), and spruce (*Picea* spp.). Mountains abruptly transitioned to short-grass prairie and limber pine (*Pinus flexilis*) savanna habitats along the eastern edge of the Rocky Mountains. Non-forested alpine habitats generally occurred above 2,000 m (Craighead et al. 1982). Primary fruit-bearing shrubs important to the diet of grizzly bears during summer and fall included huckleberry (*Vaccinium* spp.), soapberry (*Sheperdia* spp.), mountain ash (*Sorbus* spp.), hawthorn (*Crataegus douglasii*), and serviceberry (*Amanchier alnifolia*).

METHODS

Capture Methods and Monitoring Protocol

We captured grizzly bears using leg-hold snares and culvert traps, by helicopter darting, and in some instances, we darted and immobilized bears over baits. We followed the handling and immobilization procedures found in the Montana Animal Care and Use Committee protocols for grizzly bears and black bears (Montana Fish, Wildlife and Parks 2004). We tagged all bears subcutaneously with passive transponder tags and pulled a premolar tooth for age determination (Stoneberg and Jonkel 1966).

We fitted female grizzly bears $\geq$2 years old with a variety of radio-transmitters and duty cycle configurations, all of which had 6-hr mortality sensors. We used standard very high frequency (VHF) neck-mounted collars (Telonics, Inc., Mesa, AZ) and VHF ear-tag transmitters (Advanced Telemetry Systems, Inc., Isanti, MN) on some bears. We used 3 types of Telonics Global Positioning System (GPS) collars: standard GPS (TGW-4500; Telonics, Inc.), GPS-Argos (Models TGW-3580 and TGW-3583; Telonics, Inc.), and spread-spectrum collars (SST; TGW-3690; Telonics, Inc.). All GPS collars were programmed to obtain a location once every 1–4 hr. We programmed the GPS units on these collars to turn off during the normal winter denning period to preserve battery life (early Nov through early Apr). We equipped GPS collars with automatic release mechanisms, allowing the collars to release from the bear after 2 years and 3 years for subadults and adults, respectively.

We distributed our sample of radio-collared females in proportion to preliminary estimates of relative grizzly bear density across the study area, using the distribution of bears detected at DNA hair traps in 2004 (Kendall et al. 2009). We then calculated relative density for 11 predefined capture zones (Fig. 1). We established a goal of monitoring a minimum of 25 radio-marked females annually, allocated by population density in each capture zone. If, for example, 20% of the bears detected at DNA hair traps occurred in a particular capture zone, then we attempted to place 20% of the radio-marked sample in that zone. We established a goal of monitoring 2 females per year in each Canadian province because there were no estimates of population density in those areas when our study began. To account for movement of bears among capture zones, we examined the 100% minimum convex polygon home range (Mohr 1947) of each bear annually and determined the proportion of the range in each capture zone. We then compared the relative proportions of these ranges per capture zone to the desired proportion based on population density and made adjustments to our capture effort annually.

We chose specific capture sites within each capture zone while avoiding certain private properties. These properties were known to regularly attract grizzly bears seeking anthropogenic foods, and we suspected that survival rates of these bears would not be representative of the female population at large. However, we required a method for such females to enter our dataset under certain circumstances. To do so, we adopted the definitions and methods of Schwartz et al.

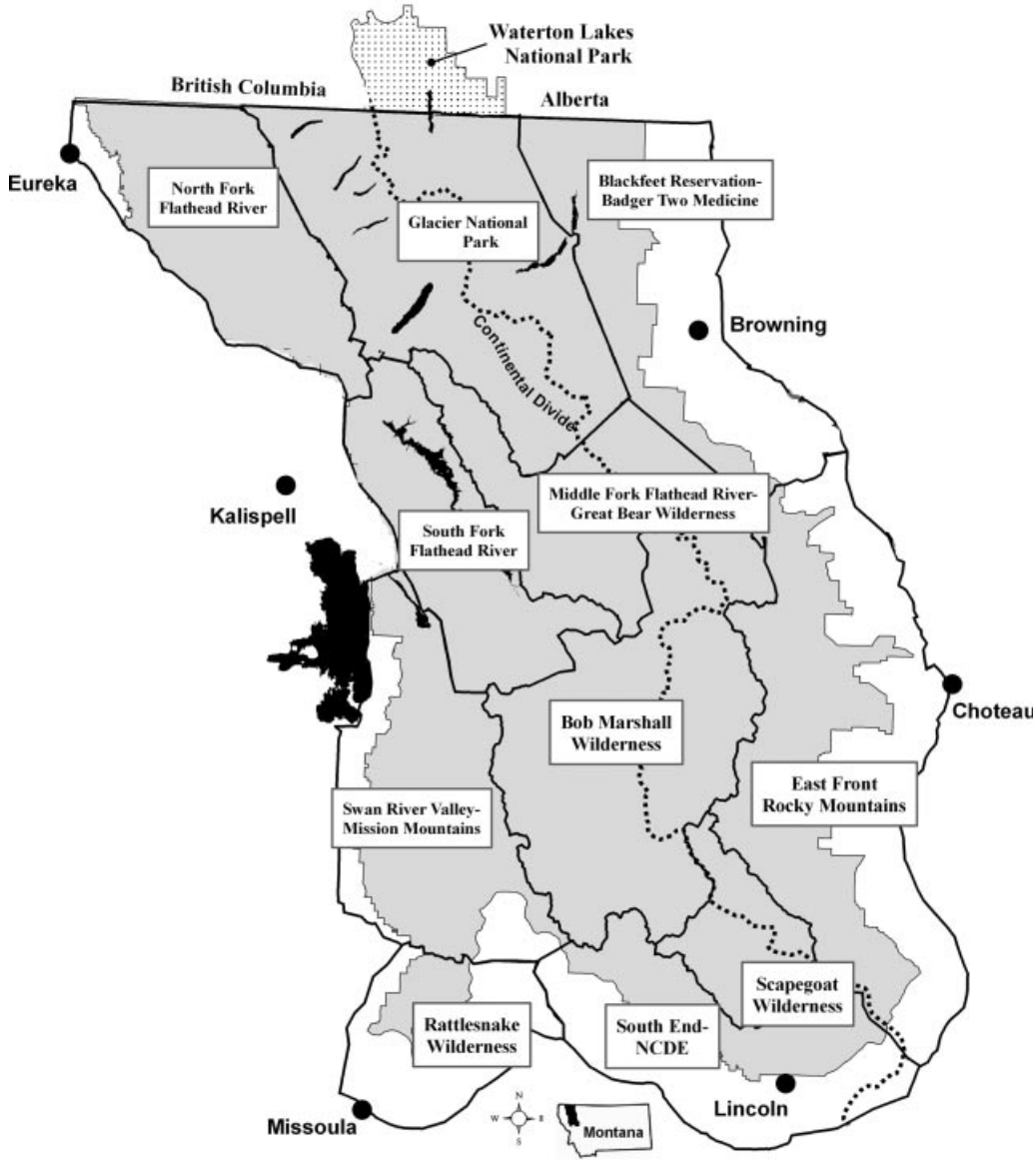

Figure 1. Zones within the Northern Continental Divide Ecosystem in Montana used to capture and monitor female grizzly bears from 2004 to 2009. The study area extended into the Canadian provinces of British Columbia and Alberta. The shaded area is the federal Recovery Zone (U.S. Fish and Wildlife Service 1993).

(2006*c*). We defined females first captured and radio-collared at a site intended for research as research females. Females first captured and radio-collared by bear managers at a bear–human conflict site were termed conflict females, whether or not they were positively implicated as having caused the conflict. A conflict bear could become a research bear if later captured at a research site. Conversely, research females captured at a conflict site retained their place as a research bear if wearing a functional radio collar at time of conflict capture. Research females whose collars had either failed or dropped off, and who we later captured at a conflict site, were reclassified as conflict bears.

Survival Analyses

Dependent young survival.—We defined dependent offspring (cubs of year [COYs] and yearlings) as bears in their first and second year of life, respectively, and determined their fate from visual observations during ground monitoring or aerial telemetry flights. We assumed COYs had died when we no longer observed them with their mother, or when their mother died. For bears residing on the west side of the Continental Divide, we assumed yearlings had died if they disappeared between observations, or when their mother died. East of the Divide, we assumed that yearlings disappearing between observations dispersed unless there was evidence of death.

We followed Schwartz et al. (2006*b*) to estimate COY and yearling survival using the nest success procedure of Dinsmore et al. (2002) in Program MARK (White and Burnham 1999). This technique is suited for intermittent observations of dependent offspring. To estimate survival, we required 3 dates: 1) the first date a female with the young was

seen (time i); 2) the last date the young were known to be present with their mother (time j; for young that survived to be yearlings, time j was the start of their second winter of hibernation); and 3) the last date the mother was monitored (time k). For young that survived the interval, time k = time j. In those cases where dependent offspring died, time k was the first date of observation of the female without young. We then coded each offspring as alive or dead.

We estimated survival of dependent offspring for 3 time periods. The first period was when offspring were COYs. This period began on the date of our first observation of a COY litter following den emergence in the spring (Julian day 120, or 30 Apr) and ended on the date of our last COY observation prior to den entry (Julian day 307, 3 Nov). The second period was the winter denning period. The denning period began on 4 November (Julian day 308) and ended on 12 April (Julian day 102). The third period was when offspring were yearlings and began on 13 April (Julian day 103) and ended on the last day we observed a yearling litter (Julian day 316, or 12 Nov). To use the nest survival module in Program MARK, we reset the start day to day 1 (Julian day 120) and concluded analyses on day 562 (12 Nov). Therefore, the lengths of the COY, denning, and yearling periods were 188 days, 161 days, and 213 days, respectively.

The nest survival method as calculated in Program MARK (White and Burnham 1999) estimates the daily survival rates (DSR) during each time period. We converted the DSR for each period into survival rates for the COY and yearling period following this convention. For the COY period, survival rate = DSR_{COY}^{188}, whereas for yearlings we calculated survival as DSR_{yrling}^{213}.

Survival of individual dependent offspring within a litter may not be independent. Dependence among litter-mates causes overdispersion, which will bias the variance of estimates, although not the estimates themselves (Schwartz et al. 2006*b*). To quantify overdispersion (i.e., $\hat{c}$), we followed the methods of Bishop et al. (2008). We used the bootstrap procedure in Program MARK (White and Burnham 1999), and bootstrapped on litters, then estimated $\hat{c}$ as the ratio of the bootstrapped variance of survival derived from 1,000 replicates to the theoretical variance of survival. We considered $\hat{c} > 1$ as an indication of overdispersion (Bishop et al. 2008) and used the adjustment to correct the uncertainty in our COY and yearling survival estimates.

Independent female survival.—We generally began monitoring radioed females in early April and concluded in November. We did not routinely monitor bears during the denning season. We used aerial and ground telemetry to determine the status (dead or alive) of females at least once per month as weather permitted. Additionally, we ascertained the status of females wearing GPS-Argos collars once per week by examining serial locations via internet downloads. When bears did not appear to move over a 24-hr period, we investigated the location to ascertain whether the bear had died. We attempted to investigate potential bear mortalities within 2 weeks of receiving a mortality signal. For dead bears, we conducted preliminary necropsies in the field and collected relevant samples for laboratory analyses. If feasible, we retrieved whole carcasses from the field and sent the remains to the Montana Fish, Wildlife and Parks laboratory for further analyses.

We classified bears fitted with GPS or GPS-Argos collars as alive during each month that ≥1 GPS fix was obtained, even if the bear was not monitored via VHF telemetry during that month. Thus, we ascertained monthly fate for these bears retrospectively by examination of telemetry data after we retrieved and downloaded the shed collar. We omitted from our survival analysis 1 bear that died within 7 days of capture and whose death we suspected was capture-related.

We estimated survival of independent subadult and adult females using the staggered-entry Kaplan–Meier method (Pollock et al. 1989) within Program MARK using the logit scale. An individual's encounter history began the month and year it was first captured and concluded the month and year it was censored or died. We coded bears as either alive, dead, or censored each month. During the active season, we considered a bear alive during a 2-month gap in telemetry data if we knew it was alive before and after the gap. If the gap in data exceeded 2 months during the active season, we censored bears for those months. We classified bears as alive during the denning months if we knew they were alive the previous October or November and if they emerged from dens wearing a functional radio collar.

Reproduction

We determined the reproductive status of each adult female visually during telemetry sessions. We conducted observation flights in early spring to ascertain which females had dependent offspring and the number of offspring per litter. We did not know with certainty the exact number of COY in each litter immediately upon their exit from winter dens. Therefore, some COY mortality may have occurred after den emergence and prior to our first observation, which would bias our estimates of litter size low (Schwartz et al. 2006*b*). To account for this, we used a correction factor to estimate litter size at the time of spring den emergence using our DSR_{COY} estimate, the number of COY observed, and the size of each litter (Schwartz et al. 2006*b*). We calculated a 50-day period between our earliest COY litter observation and the mean date of all COY observations. We first calculated the total number of COY (total COY) that could have been alive at den emergence as: n COY observed/ DSR_{COY}^{50}. We calculated the mortality-adjusted mean litter size as: total COY/n litters. We used the delta method to calculate the variance and confidence intervals for this adjusted litter size.

We adopted the method of Schwartz and White (2008) to estimate the likelihood that a female ≥3 years old in a given reproductive state in 1 year would transition to a different state the following year. In a given year, a female may be in 1 of the following states: no young (N), with dependent COY (C), with dependent yearlings (Y), or with dependent 2-year-olds (T). Therefore, we examined 10 biologically possible transitions between states: N → N, N → C, C → N, C → Y, C → C, Y → T, Y → C, Y → N, T → N, and T → C.

We calculated stable state probabilities following Schwartz and White (2008) using the multi-state model in Program MARK (White and Burnham 1999). We calculated confidence intervals for each reproductive state by bootstrapping (Efron and Gong 1983) as described by Schwartz and White (2008). We then calculated the reproductive rate (female cubs/female/year) (m_x) by multiplying our mortality-adjusted mean litter size by the stable state proportion of female bears ≥3 years old in state C (Schwartz and White 2008). We assumed a sex ratio of 50:50 in COY litters.

Our sample size was insufficient to estimate the age of primiparity using the method of Garshelis et al. (1998). We therefore report the mean age of primiparity for those females we knew had not previously produced litters, recognizing that the estimate would likely be younger than the true average age.

Asymptotic Rate of Population Growth, Stable Age Structure, and Uncertainty

To compute the asymptotic rate of population growth (λ) during the study period, we created a standard, dynamic life table, solved iteratively for r (i.e., the intrinsic rate of growth), using Microsoft Excel (Microsoft, Redmond, Washington, D.C.) and the add-in PopTools (PopTools version 3.1, www.poptools.org, accessed 02 Feb 2010). We calculated λ as e^r. We recognized that this deterministic formulation was biased high, with the magnitude of bias proportional to the temporal variance in vital rates. However, we lacked the sample size needed to isolate sampling variance from total variance, and thus had no way to estimate true temporal variance. As we discuss below, however, we have justification for believing the upward bias in deterministic λ was likely to be modest (Harris et al. 2006). Our oldest known-age female was 27 years. Therefore, for life table analysis, we assumed that all females died after age 27. We also estimated the stable age structure of the female population from our Leslie matrix using PopTools.

We developed approximate confidence intervals on λ to reflect the sampling variance in each of our vital rates by iterating life tables created using the empirical distribution of each rate in a Monte Carlo approach (Alvarez-Buylla and Slatkin 1991, 1993, 1994). We used the distributions of each vital rate as estimated from Program MARK on the logit scale, which included both process and sampling variance. To minimize the negative biases in λ caused by Jensens' inequality (Ruel and Ayres 1999), we adjusted means and variances so that when back-transformed, they approximated their means and 95% confidence limits on the real scale. We ran 10,000 Monte Carlo iterations of the life table, defining confidence limits of λ empirically from the resulting distribution.

RESULTS

COY and Yearling Survival

We followed the fate of 60 COY and 34 yearlings, and documented 14 COY and 7 yearling mortalities. We assumed 6 of 14 (42.8%) COY deaths, following the death of their 3 mothers. For survival analyses of these offspring, we used a $\hat{c}$ adjustment of 2.9206 in Program MARK to account for over-dispersion. Our estimates of DSRs for COY and yearlings were 0.99739 and 0.99820, respectively (Table 1). Estimates of survival for the active season were 0.612 (95% CI = 0.300–0.818) for COYs and 0.682 (95% CI = 0.258–0.898) for yearlings. The survival rate of COYs during the 50-day period between spring den emergence and the mean date of first COY litter observation was 0.878 (95% CI = 0.768–0.937).

Independent Female Survival

Our annual sample sizes of radio-collared independent females from 2004 to 2009 were 13, 28, 31, 33, 34, and 42 bears, respectively. In total, we monitored 83 independent females for 1,472 months. Four females transitioned from the conflict subsample into the research sample, none of which died in 102 months of monitoring. One female originally in the research sample later became part of the conflict subsample. We had strong evidence that radio collars malfunctioned on 6 individuals, and we censored them during the month that contact was lost. Five of these failures were of GPS collars, 3 of which were from the same manufacture batch and were deployed in the same year and in the same general area. One VHF collar transmitted erratic pulse rates and then failed. Our evaluation of the location of home ranges relative to capture zones showed that some zones were sampled close to the relative population density, whereas several were either under-sampled (Glacier National Park) or over-sampled (East Front-Rocky Mountains; Table 2).

No independent females died in winter dens, whereas 3 subadults and 5 adults died during the active season. Four mortalities were known to be human-caused, 1 died naturally, and we could not determine the cause of death in 3 instances. Of the 4 known human-caused deaths, 1 was a subadult mistakenly killed by a black bear hunter. We classified 1 death as malicious. The remaining 2 involved defense-of-life situations, both of which were females with COY litters. Four of 8 mortalities occurred in the North Fork Flathead River capture zone. The remaining 4 deaths occurred, 1 each in the Swan River Valley/Mission Mountains, South Fork Flathead River, Blackfeet Reservation/Two Medicine, and East Front-Rocky Mountain zones. Our estimate of annual subadult female survival was 0.852 (95% CI = 0.628–0.951). We

Table 1. Daily survival rate estimates and survival rates during the active period for grizzly bear dependent cub of year (COY) and yearlings in the Northern Continental Divide Ecosystem, 2004–2009.

		Daily survival rate (DSR)				Active period survival rate			
Age	n	Estimate	SE	−95% CI	+95% CI	Estimate	SE	−95% CI	+95% CI
COY	60	0.99739	0.00093	0.99363	0.99893	0.61193	0.10765	0.30078	0.81827
Yearling	34	0.99820	0.00090	0.99365	0.99949	0.68199	0.13222	0.25769	0.89776

Table 2. Distribution of radio-collared female grizzly bear home ranges relative to population density in 11 capture zones, Northern Continental Divide Ecosystem (NCDE), 2004–2009.

Capture zone	% Relative population density[a]	% Cumulative home ranges	% Deviation of cumulative home range from relative population density
Glacier National Park	38.5	24.0	−14.5
Blackfeet Indian Reservation-Badger Two Medicine	11.1	9.5	−1.6
North Fork Flathead River	10.5	16.7	6.2
Middle Fork Flathead River-Great Bear Wilderness	9.9	7.0	−2.9
South Fork Flathead River	9.3	8.0	−1.3
Bob Marshall Wilderness	8.5	3.3	−5.2
East Front-Rocky Mountains	5.8	18.9	13.1
Scapegoat Wilderness	3.2	2.5	−0.7
Swan River Valley-Missions Mountains	2.4	3.6	1.2
South end-NCDE	0.9	6.4	5.5
Rattlesnake Wilderness	0.0	0.0	0.0

[a] K. Kendall, U.S. Geological Survey, unpublished data.

estimated annual adult female survival at 0.952 (95% CI = 0.892–0.980; Table 3).

Reproduction

Our observed mean litter size from 30 COY litters was 2.00 COY/litter (SE = 0.127, 95% CI = 1.74–2.26). We observed litters of 2 most commonly (53.3%), whereas 23.3% of our observations were of 1 COY and 23.3% were of 3 COYs. We observed 6 COY litters of ≥2 offspring that experienced mortality, 2 of which were partial-litter loss. Our mortality-adjusted litter size was 2.27 COY/litter/year for both sexes or 1.13 female COY/litter/year. Mean age of primiparity was 5.4 years ($n = 10$, 95% CI = 4.3–6.5). Our youngest female observed with a COY was a 4-year-old.

We obtained 95 reproductive state transitions from 53 female grizzly bears who were ≥3 years old (Table 4). We observed transitions from N → N ($n = 26$) and from N → C ($n = 24$) most frequently. We observed 4 cases of females transitioning from 3 years to 4 years old; 1 transitioned from N → C, whereas the remaining 3 individuals transitioned from N → N. We recorded 3 instances of yearling litters transitioning back to COY litters. Two of these 3 cases involved yearlings leaving their mother during the spring, and in the third case, the entire yearling litter died. We estimated that the probabilities of females ≥3 years old transitioning from N → N as 0.510, from N → C as 0.490, and from C → C as 0.111 (Table 4).

From our stable state analyses, we estimated the proportions of females ≥3 years old in each reproductive state (Table 5). The proportion of adult females with COY litters was 0.322 (95% CI = 0.262–0.382). This proportion, used in conjunction with the mortality-adjusted litter size of 1.14 female COY/litter/year, provided an m_x estimate of 0.367 (95% CI = 0.273–0.461).

Asymptotic Rate of Population Growth and Stable Age Distribution

Our mean estimate of λ, produced by the deterministic life table (Table 6), was 1.031. Using the variability in vital rates, approximate 95% confidence limits were 0.928–1.102, and 90% confidence limits were 0.945–1.092. Approximately 71.5% of the simulations produced a $\lambda \geq 1.0$. From our stable age distribution calculations, we estimated that 31%, 19%, and 50% of the female population were dependent offspring, subadults, and adults, respectively. We estimated that 10% of the female population ≥3 years old were age 3.

DISCUSSION

Our results suggested that, on average, the NCDE population of grizzly bears increased at approximately 3% during the period 2004–2009. Our annual records of female mortality in the NCDE further supported the likelihood that the trend was positive. From 2004 to 2009, an average of 5 females died from human causes annually, from a female population estimate of 471 (95% CI = 427–531) individuals in 2004 (Kendall et al. 2009). Our population trend finding was comparable to several other areas such as the Greater Yellowstone Ecosystem (λ = 1.042; Harris et al. 2006) south of the NCDE and the Banff National Park-Kannanaskis Country area of Alberta, Canada (λ = 1.042) north of the NCDE (Garshelis et al. 2005). Population data for the non-parklands of central Alberta (Boulanger and Stenhouse 2009) are more troubling. Vital rates from a sample of bears in this area were insufficient for population growth ($\bar{x}$ cub survival = 0.56, $\bar{x}$ subadult female

Table 3. Annual survival of 83 independent subadult and adult female grizzly bears in the Northern Continental Divide Ecosystem, 2004–2009.

		Annual survival parameter			
Ageclass	n	Estimate	SE	−95% CI	+95% CI
Subadult[a]	26	0.851	0.079	0.628	0.951
Ad[a]	65	0.952	0.021	0.892	0.980

[a] Of the 83 females used to estimate survival, 8 provided survival data both while a subadult and as an adult. Therefore, sample sizes do not equal 83.

Table 4. Reproductive state transition probability estimates for female grizzly bears (≥3 years old) in the Northern Continental Divide Ecosystem, 2004–2009.

	Probability of transitioning from current state to next reproductive state							
	N[b]		C		Y		T	
Current reproductive state[a]	*n*	*P*	*n*	*P* (SE)	*n*	*P* (SE)	*n*	*P* (SE)
N	26	0.510	24	0.490 (0.070)	0[c]	0	0	0
C	1	0.040	3	0.111 (0.060)	23	0.852 (0.068)	0	0
Y	4	0.333	3	0.167 (0.111)	0	0	6	0.500 (0.144)
T	1	0.200	4	0.800 (0.180)	0	0	0	0

[a] N = lone female, C = female with COY litter, Y = female with a yearling litter, and T = female with a 2-year-old litter.
[b] Probabilities for the N state were calculated by difference.
[c] A transition that was not biologically possible.

survival = 0.74, $\bar{x}$ adult female survival = 0.95, and $\bar{x}$ reproductive rate = 0.20). The grizzly bear population in this area was designated as threatened in June 2010 (Alberta Sustainable Resource Development and Alberta Conservation Association 2010).

To the best of our knowledge, this is the first brown bear study to, a prori, geographically distribute a sample of radioed bears based on relative population density. Stratification is a recommended sampling technique when animals are not evenly distributed throughout a survey area (Caughley 1977). Therefore, our sampling protocol provided a means to weigh reproductive and survival rates, used to calculate trend, by bear density. However, we could not completely attain our goal of matching sample sizes of radioed females in capture zones with bear density, because we could not predict how radioed bears would move among capture zones following capture.

We had difficulty observing cub litters at time of den emergence because females denned in mountainous areas where unpredictable spring weather conditions made observation flights difficult. Further, it was difficult to schedule observation flights to observe litters, as the timing of den emergence was unpredictable; emergence has been shown to vary annually in the NCDE by 3–4 weeks (Mace and Waller 1997). Therefore, our observations of cub litter sizes were undoubtedly biased low, because of postemergent mortality we did not observe. We accounted for this by adjusting our estimate of cub litter sizes using their DSR. Our unadjusted mean litter size was 2.0 cubs/litter/year, and our mortality-adjusted estimate was 2.27 cubs/litter/year. This adjusted litter size compares favorably to other estimates of 2.29 and 2.14 cubs/litter/year for the NCDE that were based on counts of corpra lutea from female reproductive tracts and from visual observations, respectively (Aune et al. 1994). Our reproductive rate (m_x) estimate was 0.367 (female cubs/female/year), using the mortality-adjusted litter size, and was similar to the reproductive rate estimate of 0.362 for grizzly bears in the Yellowstone National Park area (Schwartz et al. 2006*b*).

Schwartz and White (2008) provided a rationale for including 3-year-old female brown bears in the calculation of reproductive transition probabilities. Most importantly, some known-aged females bred as 3-year-olds and produced their first litter at age 4, so it was important to include those individuals who matured early in our calculations. Our 95 transition records included 4 bears (4.2%) that aged from 3 years to 4 years old, 1 of which produced cubs at age 4. Similarly, 7.7% of the records of Schwartz and White (2008) for Yellowstone grizzly bears were transitions that began at age 3. In the Yellowstone grizzly bear population, 3-year-old females comprised 5–8% of the stable-aged population ≥3 years old. For our population in the NCDE, we estimated that 3-year-olds constituted 10% of the stable-aged population of females ≥3 years old. To the best of our knowledge, there is no evidence in the

Table 5. Stable state probabilities that the female grizzly bear population (≥3 years old) was composed of no young, COY litters, yearling litters, or 2-year-old litters. Northern Continental Divide Ecosystem, 2004–2009.

	Reproductive state parameter estimates			
Reproductive state[a]	Estimate	−95% CI	+95% CI	SE
N	0.267	0.123	0.411	0.073
C	0.322	0.262	0.382	0.031
Y	0.274	0.224	0.324	0.026
T	0.137	0.056	0.218	0.041
Dependent offspring	0.596	0.496	0.696	0.051

[a] N = lone female, C = female with a COY litter, Y = female with a yearling litter, and T = female with a 2-year-old litter. The probability of having dependent offspring is the summation of the C and Y states.

Table 6. Summary of grizzly bear vital rate statistics used to derive confidence intervals for λ in the Northern Continental Divide Ecosystem, 2004–2009.

	Vital rate parameter estimates		
Vital rate[a]	Mean	−95% CI	+95% CI
COY survival (s_0)	0.6119	0.3008	0.8183
	0.6132	0.3111	0.8363
Yearling survival (s_1)	0.6820	0.2577	0.8978
	0.6833	0.3007	0.9103
Subad survival ($s_{2–4}$)	0.8518	0.6282	0.9514
	0.8516	0.6429	0.9609
Ad survival (s_{5+})	0.9529	0.8918	0.9803
	0.9478	0.8856	0.9816
Fecundity (m_x)	0.3668	0.2726	0.4611
	0.3665	0.2728	0.4624

[a] For each rate, the upper set of values provides the estimated mean and confidence intervals produced by back-transforming the original values produced by Program MARK; the lower set of values provides the values realized by Monte Carlo simulations (n = 10,000), after adjustments, back-transformed to the real scale.

literature of 3-year-old female brown bears with cub litters (Schwartz et al. 2003).

The age of primiparity varies geographically in brown bear populations (McLellan 1994). Our youngest age of primiparity was 4 years; similar to observations from other brown bear populations (Aune et al. 1994, McLellan 1994, Mace and Waller 1998, Schwartz et al. 2003, Schwartz et al. 2006*a*). Our oldest known-aged female was 27 years old and produced cubs the previous year. In our estimate of population trend, we assumed all females died after age 27, although females are known to live longer (Schwartz et al. 2003). We do not believe that omitting these older females influenced our estimate of population trend, as very few individuals this old would be present in the population.

We assumed yearlings that disappeared between observation flights dispersed rather than died, for bears residing on the east side of the Continental Divide. Dispersal of yearlings is well documented on the east side (M. Madel, Montana Fish, Wildlife and Parks, unpublished report) and in other brown bear populations (McLellan and Hovey 2001, Dahle and Swenson 2003). Mace and Waller (1998) did not observe yearling dispersal to the west of the Divide. It has been documented that age of maturity in brown bears is correlated with body size and diet (Stringham 1990, Hilderbrand et al. 1999). On the east side of the Divide, there is a concentrated source of food available to grizzly bears. Each spring for the past 20 years, bear managers remove the carcasses of approximately 100 livestock from ranches and redistribute them in more remote areas where they are fed upon by bears. These carcasses serve to concentrate both males and females during the breeding season and may promote yearling dispersal as found by Dahle and Swenson (2003). This high-protein food source has also led to a larger body size for bears on the east side of the Continental Divide relative to bears elsewhere in the NCDE.

Two related problems arise when using Monte Carlo simulations to estimate $\overline{\lambda}$ from a set of vital rate distributions. The first is that survival rate distributions are not normally distributed, and thus must be simulated on the scale in which they were produced (logit, in our case) and then, for input into a life table, they must be transformed back to the real scale. Because survival distributions are asymmetric, back-transformation of the original values results in a biased distribution of real values (because of Jensen's inequality, see Ruel and Ayres 1999). In general, it is not possible to preserve both the mean and variance of a distribution on the original scale when back-transformed to the real scale. Thus, some post hoc approximation is necessary to avoid simulated life tables having different mean parameters than those found by field sampling. We inputted various trial values of means and variances on the logit scale until Monte Carlo simulations reproduced means and confidence intervals on the real scale that were close ($\overline{x}$ discrepancy = 0.0016, maximum = 0.0051 for mean parameter values; $\overline{x}$ discrepancy = 0.0117, maximum = 0.0430 for 95% confidence limits) to those produced by Program MARK in the original analyses.

Secondly, Jensen's inequality affects inference from a distribution of life tables. The mean of a distribution of such life tables (or matrices) is not equal to a single life table (or matrix) produced by the mean values (the difference being proportional to the magnitude of variation in each vital rate, weighted by the elasticity of each rate). We know of no solution to this second problem, except to note that the mean of the simulated $\hat{\lambda}$ (i.e., $\hat{\lambda}$) will be lower than the single λ produced by the best (i.e., deterministic) life table. It is possible to gain an appreciation for the probable magnitude of bias in the deterministic estimate of λ (1.0306) by careful inspection of these stochastic estimates. The reduction in apparent rate of growth caused by adding the observed level of variability was (1.0276–1.0235) = 0.0041 (i.e., 0.4% growth/year). We do not know how much of the variation was process variance and how much was sampling variance. In Yellowstone, Haroldson et al. (2006) were able to estimate the process-only standard deviation of adult female survival (assuming unresolved animals were censored when lost, 0.950) as 0.013. To generate confidence limits on λ, Harris et al. (2007:170) used the total variation in the same rate to estimate the standard deviation of adult female survival as 0.020. In the Yellowstone data, it appeared that slightly more than half the total variation in female survival was process variation. Because sample sizes in Yellowstone (1983–2001) were larger than in the NCDE during 2004–2009, it seems reasonable to assume that sampling variation would exert a proportionally larger effect here. However, even if all variation was process variation (i.e., no sampling variation at all), we would not expect the bias in the deterministic λ (1.0306) to exceed the reduction observed (i.e., 0.0041–1.0235) when adding the total variability to a life table where the expected λ was 1.0276. Thus, even without knowing the magnitude of process variation, it seems likely that the best estimate of λ implied by the data is between 1.025 and 1.030.

MANAGEMENT IMPLICATIONS

The results of Kendall et al. (2009), MacHutchon et al. (2008), and Hovey and McLellan (1996), coupled with this study, show a growing population of more than 1,000 bears in and adjacent to the NCDE. This is in contrast to a crude population estimate of 440–680 grizzly bears present in the United States portion of the study area at time of listing under the Endangered Species Act (U.S. Fish and Wildlife Service 1993) in 1975. Kendall et al. (2009) also suggested that their measures of high genetic diversity coupled with an expanded distribution of bears were consistent with a positive trajectory in population trend in this population.

We concur with Kendall et al. (2009) that grizzly bear recovery efforts for the NCDE have been generally successful. Population and habitat management programs that may have contributed to this success include proactive management of bear–human conflicts, programs designed to manage mortality within sustainable levels, and habitat guidelines designed to maintain security. These and other programs will require an adaptive management approach (Enck et al. 2006) which includes continued efforts to monitor population

trend and other vital rates. Our study represents 6 years of demographic data, and confidence intervals for our estimates of vital rates and trend were relatively wide. To improve these estimates, Harris et al. (2011) suggest that increased the monitoring of recruitment and juvenile survival may be most beneficial, as these parameters tend to vary more widely than does adult survival. Also, managers should recognize the inherent uncertainty in trend estimates, as confidence intervals for λ usually bound 1.0 in brown bear studies, unless the population size changes rapidly (Harris et al. 2011). We suggest continued monitoring of radioed bears in the NCDE to better understand population trend. Continued investment in this monitoring designed within an experiment context will provide managers the necessary information to judge the success of future grizzly bear population and habitat management actions and possibly the tools to assess the impacts of environmental change (e.g., climate change).

ACKNOWLEDGMENTS

We wish to thank the following people for both administrative and field support: C. Amacher, S. Anderson, C. Barboulatos, J. DeHerrera, J. Gude, K. Graham, D. Hoerner, J. Lowe, D. Mucklow, K. McDonald, J. Northrup, E. Peterson, L. Roberts, H. Reich, D. Reich, C. Smith, and J. Williams. We thank K. Kendall (U.S. Geological Survey) for providing the unpublished data we used for estimating relative population density of grizzly bears. We also wish to thank G. C. White and S. Cherry for their assistance with vital rate modeling approaches.

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Associate Editor: Scott McCorquodale.