Grizzly Bear Demographics in the Northern Continental Divide Ecosystem 2004–2014

Research Results & Techniques for Management of Mortality

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GRIZZLY BEAR DEMOGRAPHICS IN THE NORTHERN CONTINENTAL DIVIDE ECOSYSTEM, MONTANA: RESEARCH RESULTS (2004–2014) AND SUGGESTED TECHNIQUES FOR MANAGEMENT OF MORTALITY

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The demographic information presented herein supersedes that of Mace et al. (2012) and that presented in the 2013 Draft Grizzly Bear Conservation Strategy for the NCDE.

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EXECUTIVE SUMMARY

In 2004, an interagency team was established by state, federal, and tribal officials to monitor the survival and reproductive rates of radio-marked female grizzly bears and estimate population trend throughout the Northern Continental Divide Ecosystem (NCDE). Herein, we report distribution, mortality levels, population vital rates, and population trend during 2004–2014, and provide a technical framework for the management of grizzly bear mortality levels to meet population management goals. Most analyses relied on the capture, radio-marking, and monitoring of independent (≥2 years old) grizzly bears throughout the Demographic Monitoring Area (DMA; USFWS 2013), a 42,600 km^2 area comprised of the Primary Conservation Area (PCA; equivalent to the Recovery Zone) and Zone 1 (roughly correlating with a 10-mile buffer around surrounding the PCA) within the NCDE. Mortalities and bear locations were also recorded outside of the DMA.

During 2004–2014, we documented presence of reproductive females (with dependent cubs, yearlings or 2-year-olds) within all 23 Bear Management Units (BMUs) of the PCA and all 7 supplementary BMUs in Zone 1. On average, at least 17 of 23 (74%) BMUs and 5 of 7 (71%) supplementary BMUs were occupied by reproductive females annually. Using a 6-year running tally, the demographic standards for occupancy within the PCA (USFWS 1993) were met each year beginning in 2009. Using all verified grizzly bear locations during 2004–2014 and the ordinary kriging method of Bjornlie et al. (2014), we estimated the total distribution of grizzly bears in the NCDE to be 55,200 km^2, extending beyond the DMA in all directions.

We documented 169 (77 F, 89 M) known or probable mortalities of independent grizzly bears within the DMA during 2004–2014. Inflating this estimate using the Bayesian method (Cherry et al. 2002), our estimate of total independent bear mortalities within the DMA was 338 for the study period or a mean of 30.7 total, 13.8 female, and 16.9 male mortalities per year. We documented an additional 18 (5 F, 13 M) known or probable independent mortalities that occurred outside of the DMA during this period, which we used to estimate an additional 1.6 total, 0.5 female, and 1.2 male mortalities/year outside of the DMA.

We monitored 169 independent females during 3,441 total months and documented 21 mortalities. Our estimated annual female survival rate was 0.951 assuming marked bears with unknown fates survived and 0.943 assuming marked bears with unknown fates died. The modeled stable-age distribution based on the mean of these two rates was consistent with field-derived estimates of population age structure. We monitored 124 independent males during 910 total months and documented

24 mortalities. Our estimated annual male survival rate was 0.916 assuming marked bears with unknown fates survived and 0.805 assuming marked bears with unknown fates died. Based on population modeling using rates within this range, we found that the modeled stable-age distribution was most consistent with field-derived estimates of age structure when male survival was set at 0.895. Therefore, our best estimates of independent female and male survival were 0.947 ($\pm$ 0.014 SE) and 0.895 ($\pm$ 0.054), respectively. We monitored cub and/or yearling survival of 176 offspring in 89 litters during 39,070 total days, and documented 65 known or probable mortalities. Annual survival estimates were 0.553 ($\pm$ 0.070 SE) for cubs and 0.639 ($\pm$ 0.080 SE) for yearlings. We detected no temporal trend in survival rates for independent or dependent bears during the 2004–2014 study period.

We documented 232 reproductive transitions (e.g., a female with cubs in one year transitioning to a female with yearlings in the following year) for 114 females and estimated the annual proportion of females with cubs as 0.287 ($\pm$ 0.031 SE). Based on observations of 110 litters for 90 females, we estimated a mean litter size of 2.10 ($\pm$ 0.050 SE). The youngest and oldest age of females observed with cubs was 4 and 26 years, respectively. Based on observations for 32 nulliparous females monitored for 1–4 years beginning at age 4, we estimated the unbiased age of primiparity (Garshelis et al. 1998) as 5.8 years ($\pm$ 0.262 SE).

Based on deterministic and stochastic population modeling of the observed vital rates, we estimated the annual population growth rate was 1.023, or 2.3% growth/year. Assuming an initial population size of 765 in 2004 (Kendall et al. 2009), the median estimated population size was 960 bears in 2014 with a 95th percentile of 946–1,089. Defining population decline as ending population size <95% of the initial population, with our stochastic modeling we estimated a 0.05% chance that the NCDE grizzly bear population declined during 2004-14.

Assuming observed reproductive rates, stochastic population modeling indicated that independent female survival rates $\geq$0.93 and male survival rates $\geq$0.86 were consistent with population stability or growth under a scenario of increased female and male mortality, and male survival rates $\geq$0.80 were consistent with stability or growth under a scenario of increased male mortality only (i.e., holding female survival at our best estimate of 0.947). This was irrespective of initial population size. Using these minimum sustainable survival rates, we calculated sustainable mortality thresholds as a function of population size and compared these estimates with the number of independent bear mortalities during 2004–2014 and model-estimated population size (based on an initial population size of 2004). These comparisons suggested that our calculated mortality thresholds would have been inconsistent with population stability or growth during 2004–2014, therefore we adjusted the mortality thresholds

downward to correspond with our observed data. Under a scenario of increased female and male mortality, our adjusted mortality thresholds for independent females and males were 2.3% and 3.0% of total population size, respectively. Under the scenario of increased male mortality only, adjusted mortality thresholds for independent females and males were 1.7% and 4.3% of total population size, respectively. Consistent with estimated population growth during 2004–2014, the mean estimated numbers of total independent bear mortalities during 2004–2014 were approximately 6 females and 10 males below these thresholds under a scenario of increased female and male mortality. Numbers of total mortalities were approximately 1 female and 21 males below theses thresholds under a scenario of increased male mortality only. These findings should prove useful for establishing mortality thresholds, assuming future rates of recruitment and dependent bear survival remain similar to our current estimates. Continued monitoring of grizzly bear survival rates (cub, yearling, independent female, and independent male), reproductive parameters (annual proportion of independent females with cubs, mean litter size), distribution, and mortality will be needed to periodically re-evaluate mortality thresholds and the status and trend of the population.

1 INTRODUCTION

Although the grizzly bear (*Ursus arctos*) was listed in the contiguous United States as Threatened under the Endangered Species Act in 1975, the population size in the Northern Continental Divide Ecosystem (NCDE) Recovery Zone was unknown at the time of listing. It was not until the late 1990s that genetic field techniques were developed that could be used to estimate population size of bears at the ecosystem level (Woods et al. 1999). In 2004, a large-scale study to estimate population size was undertaken in the NCDE using genetic tagging of grizzly bears at hair traps and rub trees (Kendall et al. 2009). Concurrent with this study, an interagency team was established by state, federal, and tribal officials to monitor the survival and reproductive rates of radio-marked female grizzly bears and estimate trend throughout the NCDE. The results of this population trend study were published (Mace et al. 2012) using data from 2004–2009. Herein, we have updated the previous analyses, using data from 2004 through 2014, and report on population vital rates, mortality levels, current distribution, and population trend. Further, we provide a technical framework for the management of grizzly bear mortality levels to meet population management goals. These findings should prove useful in developing future population management programs and monitoring protocols for grizzly bears in this ecosystem.

2 STUDY AREA

We studied grizzly bears throughout the Rocky Mountain region of northwestern Montana, including: Glacier National Park; parts of five National Forests (Flathead, Helena, Kootenai, Lewis and Clark, and Lolo); parts of the Blackfeet and Flathead Indian Reservations; Bureau of Land Management lands; state lands; and private lands. The NCDE grizzly bear population is contiguous with those in the Canadian provinces of British Columbia and Alberta, therefore some captures and monitoring occurred north of the United States in Canada.

Our study area was spatially defined by the Primary Conservation Area (PCA) and Management Zone 1 (Figure 2.1), as delineated in the Draft NCDE Grizzly Bear Conservation Strategy (hereafter Draft Conservation Strategy; USFWS 2013). The PCA, encompassing 23,118 km^2, is equivalent to the Federal Recovery Zone delineated in the Grizzly Bear Recovery Plan (hereafter Recovery Plan; USFWS 1993), where the objective is continual occupancy by grizzly bears, facilitated by maintenance of compatible habitat conditions and population criteria (Table 2.1). Zone 1, which encompasses an additional 19,484 km^2, roughly correlates to a 10-mile buffer surrounding the PCA. The objective for Zone 1, as stated in the Draft Conservation Strategy (USFWS 2013), is also continual occupancy by grizzly bears, but densities are expected to be lower than within the PCA. Together, the PCA and Zone 1 (42,602 km^2) are termed the Demographic Monitoring Area (DMA), where population monitoring data are to be collected and where finalized mortality thresholds will apply. The DMA is dominated by public lands (55% federal, 5% state, 11% tribal, and 29% private). Two regions of potential connectivity to other ecosystems exist within the DMA. The northwestern portion of Zone 1 (the Salish area) may provide connectivity with the Cabinet-Yaak Ecosystem (CYE), and the southwestern portion of Zone 1 (the Ninemile Area) may provide connectivity with the Bitterroot Ecosystem.

Zone 2, as outlined in the Draft Conservation Strategy, is the area managed for genetic connectivity between the NCDE and the Greater Yellowstone Ecosystem (GYE). It is 18,861 km^2 and is predominantly privately owned (63% private, 25% USFS, and 12% state or other federal ownership). Zone 3 consists of habitat unsuitable to support grizzly bear population growth, but it is sometimes occupied by bears that most likely originated from the NCDE population. Grizzly bear occupancy will not be encouraged in this area, but bears that occur here will not be actively removed unless they are involved in bear-human conflicts. This area is 49,201 km^2 and is also predominantly private land (78% private; 9% USFS; 4% Tribal; and 9% state or other federal ownership).
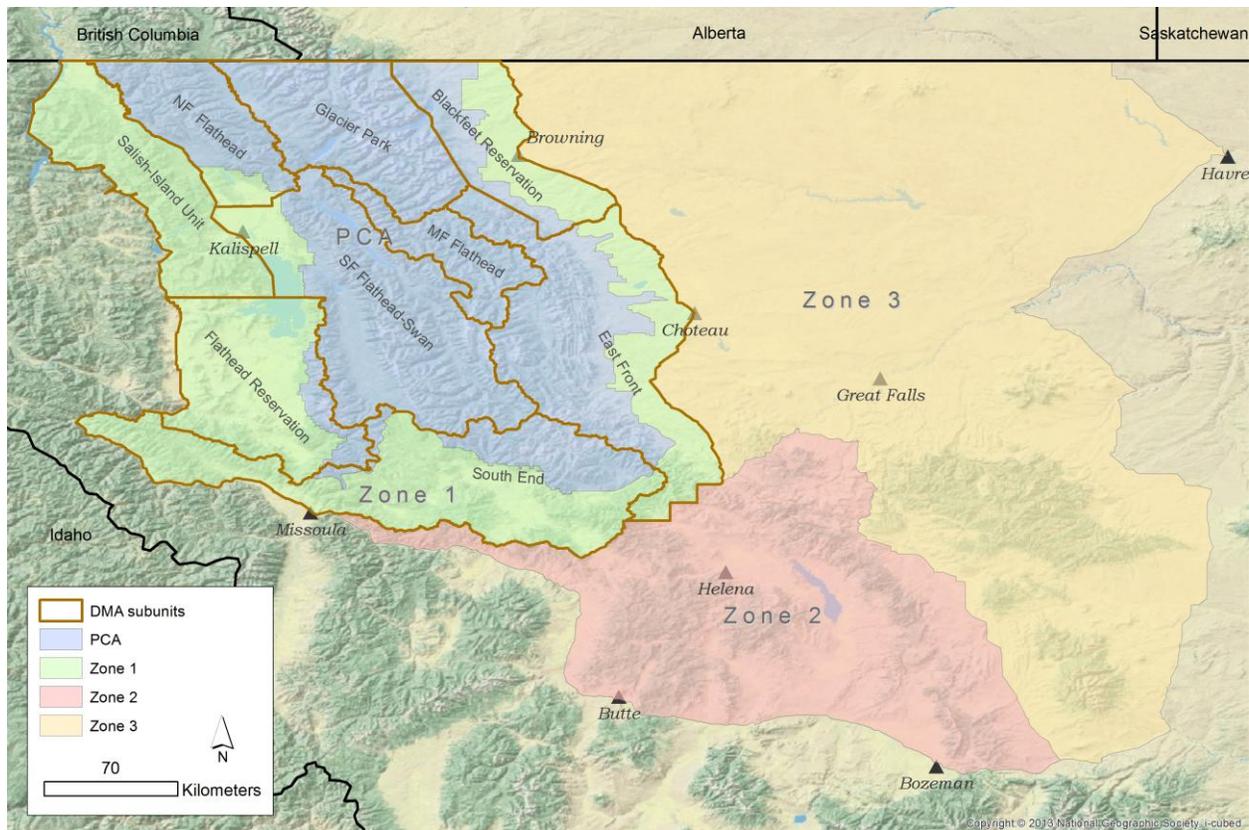
Figure 2.1. The Demographic Monitoring Area (DMA), where our grizzly bear population monitoring was conducted, consists of the Primary Conservation Area (PCA; equivalent to the Recovery Zone [blue]) and Zone 1 (green). DMA subunits (orange lines), used for localized population analyses, were based on distinct land ownerships and wildlife management authorities. Zone 2 (pink) is the area of potential genetic connectivity between the Northern Continental Divide Ecosystem (NCDE) and the Greater Yellowstone Ecosystem (GYE). Zone 3 (orange) consists of largely unsuitable habitat that may be irregularly occupied by grizzly bears.

This study area consists of rugged mountain topography shaped by glaciation. West of the Continental Divide, lower elevation habitats are dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and spruce (*Picea* spp.). East of the Divide, mountains abruptly transition to short-grass prairie and limber pine (*Pinus flexilis*) savanna habitats along the eastern edge of the Rocky Mountains. Non-forested alpine habitats generally occur above 2,000 m (Craighead et al. 1982).

We designated 9 subunits within the DMA which recognize distinct land ownerships and grizzly bear population management authorities (Figure 2.1). These are the land units to use for more localized population analyses, and the outer boundary is consistent with the boundaries of Zone 1 of the Draft Conservation Strategy (USFWS 2013). Glacier National Park subunit is managed by the National Park

Service as a wildlife preserve where grizzly bear mortality is minimized and where hunting would not be authorized. Portions of the Blackfeet Reservation and the Flathead Reservation (Confederated Salish and Kootenai Tribes) are located within the DMA, and population management authority both inside and outside of the DMA rests with their respective tribal councils. Population management within the remaining subunits would be administered by Montana Fish, Wildlife and Parks (MTFWP).

Table 2.1. Area (km^2) of zones and units used for monitoring and management of grizzly bears in the NCDE.

Name	Area (km^2)	Name	Area (km^2)
Management zones		**Bear Management Units**	
Primary Conservation Area	23,118	Murphy Lake	466
Zone 1	19,484	Upper North Fork Flathead	1,772
Zone 2	18,861	Northeast Glacier	1,675
Zone 3	49,201	Stillwater River	436
		Lower North Fork Flathead	1,349
DMA subunits		Hungry Horse	826
Salish-Island Unit	3,955	Lower Middle Fork Flathead	1,222
NF Flathead	2,784	Southeast Glacier	904
Glacier Park	4,074	Mission Range	1,398
Blackfeet Reservation[a]	2,991	Sullivan	1,035
SF Flathead-Swan	7,174	Upper Middle Fork Flathead	738
MF Flathead	1,829	Badger Two Medicine	876
East Front	7,394	Bunker	1,059
Flathead Reservation[a]	4,680	Continental Divide	797
South End	7,709	Birch Teton	841
		Big Salmon	1,366
Supplementary Bear Management Units		North Fork Sun River	669
		South Fork Sun Beaver Willow	1,065
Salish Connectivity Area	2,141	Teton Sun River	777
Flathead Valley	3,097	Rattlesnake	437
Flathead Reservation	3,426	Upper South Fork Flathead	1,017
Ninemile Connectivity Area	2,098	Monture Landers Fork	1,660
South End	4,365	Dearborn Elk Creek	752
East Front	2,725		
Blackfeet Reservation	1,607		

[a] Area of the reservation within the DMA only; a portion of the reservation extends beyond the DMA boundary.

Different from DMA subunits, Bear Management Units (BMUs) are used to assess the distribution of reproductive females within the PCA (Figure 2.2; USFWS 1993, USFWS 2013). The 23 BMUs are the same as has been historically used by land management agencies to monitor habitat condition. These BMUs are not the same as DMA subunits, as BMUs are too small in size to assign population management or mortality goals, and they cross jurisdictional boundaries. Because the BMUs were confined to the PCA, we also established supplementary BMUs within Zone 1 based on the Demographic Connectivity Areas (USFWS 2013) and DMA subunit boundaries outside of the PCA. These supplementary BMUs were generally larger than the BMUs within the PCA (Table 2.1).
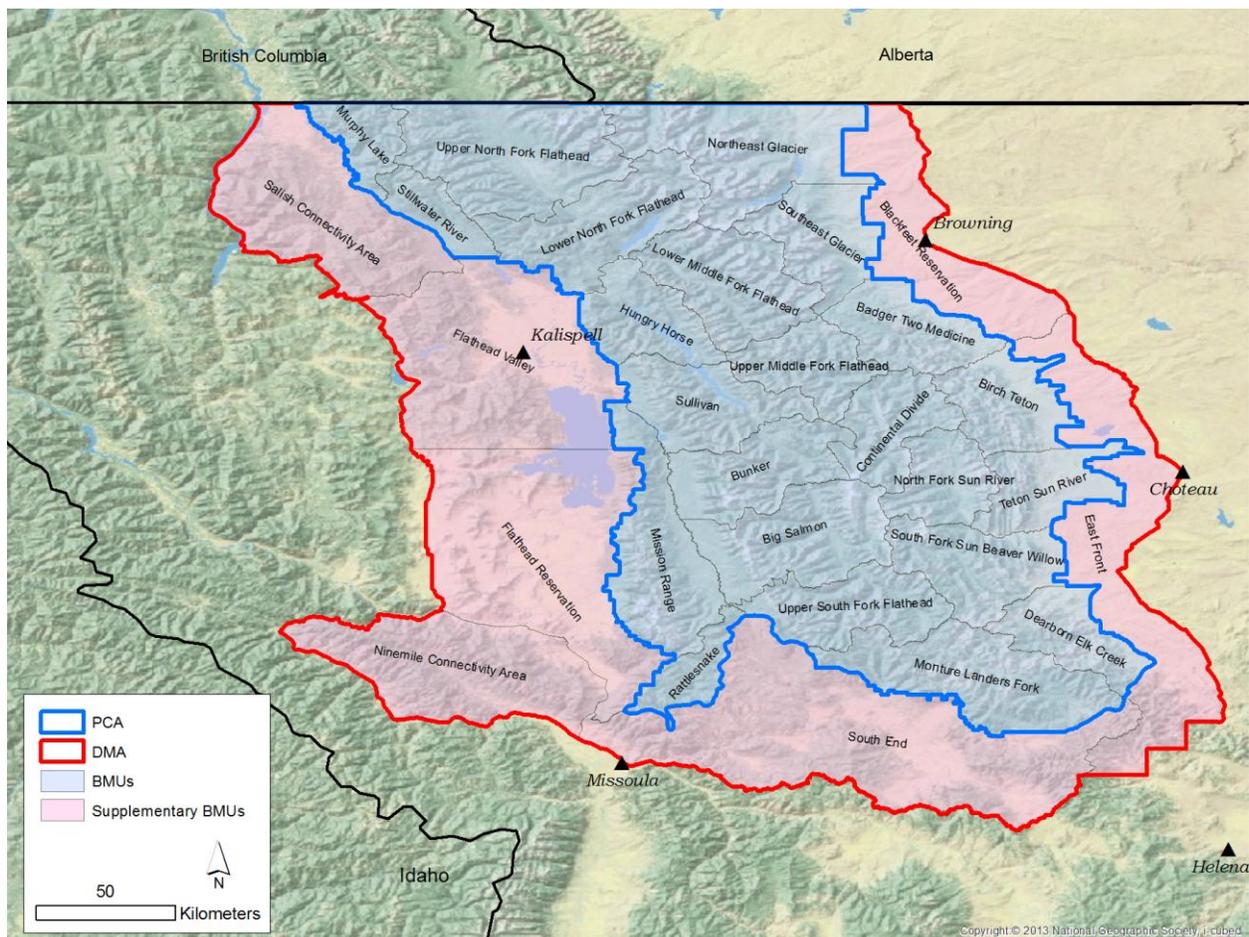
Figure 2.2. Bear Management Units (BMUs [blue]) used to assess distribution of reproductive female grizzly bears within the PCA (blue line), and supplementary BMUs (pink) used to assess their distribution within Zone 1.

3 SUMMARY OF GRIZZLY BEAR POPULATION SIZE

Our primary information on the population size of grizzly bears comes from the genetic capture/recapture studies of Kendall et al. (2008) and Kendall et al. (2009). The earlier effort was conducted in 1998 and 2000 for a region termed the Greater Glacier Area which encompassed all of Glacier National Park, the North Fork of the Flathead River, and a portion of the Blackfeet Reservation. Accounting for geographic closure, the estimated mean population size in this area was 241 grizzly bears both in 1998 and in 2000. The 1998 data indicated that 52% of the population was female, whereas the 2000 estimate (corrected for closure) suggested a ratio of 61% female to 39% male. Grizzly bear detections were 2.4 times higher within Glacier Park than outside the Park, and mean bear density was 30 bears/1000 km^2 (Kendall et al. 2008).

In 2004 Kendall et al. (2009) conducted a genetic capture/recapture study that encompassed the entire PCA and adjacent areas thought to be inhabited by bears (31,410 km^2). The mean population estimate was 765 bears (95% confidence interval [CI]: 715–831), including all age classes. The male population estimate was 295 individuals (95% CI = 276–324) and the female population estimate was 471 individuals (95% CI: 427–531), suggesting a total population skewed towards females (62%). Population density was greatest in the northern third of the PCA and generally declined southward (Figure 3.1). Mean heterozygosity across 7 genetic markers was 0.73. Kendall et al. (2009) also verified that all age and sex classes were sampled in their effort.
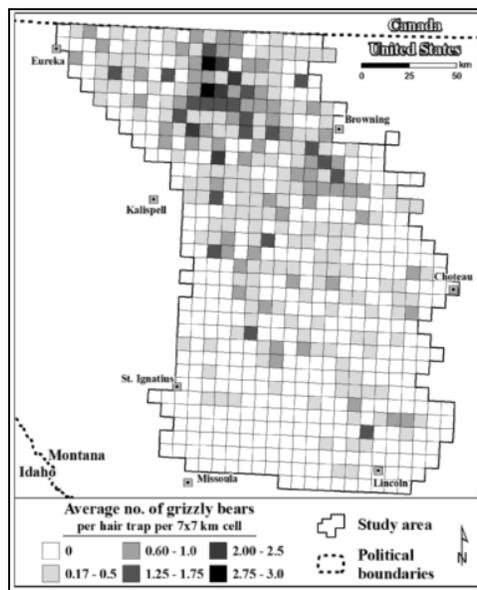
Figure 3.1. Relative density map of grizzly bears in the NCDE in 2004 (from Kendall et al. 2009).

4 RESEARCH FINDINGS

4.1 Occupancy of Reproductive Females

Adequate distribution of breeding grizzly bears throughout the NCDE is an important aspect of population recovery (USFWS 1993) and maintenance (Dood et al. 2006, USFWS 2013). The Recovery Plan (1993) and the Draft Conservation Strategy (USFWS 2013) set forth a standard for grizzly bear distribution within the PCA, based on the documented presence of reproductive females (females with dependent cubs, yearlings, or 2-year-olds) within BMUs (Figure 2.2). This standard calls for the documented presence of reproductive females in at least 21 of 23 BMUs at least every 6 years. The Recovery Plan (1993) standard also includes the provision that no two adjacent BMUs be unoccupied, and stipulates occupation of the Mission Range BMU.

Prior to 2004, efforts to document occupancy of BMUs by reproductive females relied primarily on general observations; observations and captures of bears by personnel involved in conflict management; and observations and captures of bears by personnel involved in research studies within distinct areas of the NCDE (e.g., the East Front study [Aune and Kasworm 1989] and the Swan Mountains Study [Mace and Waller 1998]). Consequently, there was a lack of consistency in data collection and survey efforts. BMUs with active research projects tended to have more observations, while less accessible BMUs tended to have fewer observations (Pac and Dood 1999). With the initiation of the grizzly bear trend monitoring program, which encompassed the entire NCDE, more consistent data on the presence of reproductive females was available. In this section, we examine occupancy by reproductive females within the DMA.

Methods

We documented presence of reproductive females within the BMUs of the PCA and within the supplementary BMUs of Zone 1 during 2004–2014, based on: visual observations of radio-marked females; verified remote camera photos; other verified visual observations; and from known or probable mortalities of family units (death of the mother, dependent young, or both). Locations of radio-marked females known to have offspring were also used to document presence.

Results

During 2004–2014, we verified presence of reproductive females within all 23 BMUs during at least 1 year (Table 4.1.1, Figure 4.1.1). On average, at least 17 of 23 (74%) BMUs were occupied by

Table 4.1.1. Documented occupancy by grizzly bear females with dependent young (cubs, yearlings, or 2-year-olds) within the 23 BMUs of the PCA and the 7 supplementary BMUs of Zone 1, NCDE, 2004-2014. Shading signifies years when occupancy was verified within a 6-year period ending with the current year.

BMU	Year										
	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Monture Landers Fork	N	Y	N	N	N	N	Y	Y	Y	Y	Y
Rattlesnake	N	N	Y	Y	N	Y	Y	N	Y	Y	Y
Upper South Fork Flathead	N	N	Y	Y	N	Y	Y	N	Y	Y	N
Mission Range	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Big Salmon	N	N	Y	Y	N	Y	Y	N	Y	Y	Y
Dearborn Elk Creek	N	N	N	N	N	Y	Y	N	Y	N	N
South Fork Sun Beaver Willow	N	N	N	N	N	N	Y	N	N	N	N
Teton Sun River	Y	Y	Y	Y	N	Y	Y	Y	Y	Y	Y
Bunker	Y	Y	Y	Y	N	Y	Y	Y	Y	Y	Y
North Fork Sun River	N	Y	N	N	N	N	N	Y	Y	N	N
Continental Divide	Y	N	N	Y	N	Y	N	Y	Y	N	N
Sullivan	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Birch Teton	N	N	Y	Y	Y	Y	Y	Y	Y	Y	N
Upper Middle Fork Flathead	Y	Y	N	Y	N	Y	N	Y	Y	Y	Y
Badger Two Medicine	Y	N	Y	Y	Y	Y	Y	Y	Y	Y	Y
Hungry Horse	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Lower Middle Fork Flathead	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Southeast Glacier	N	N	Y	Y	Y	Y	Y	Y	N	Y	Y
Lower North Fork Flathead	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Stillwater River	N	Y	Y	Y	Y	Y	Y	N	Y	Y	Y
Northeast Glacier	N	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Upper North Fork Flathead	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Murphy Lake	Y	Y	Y	Y	Y	N	Y	Y	Y	N	Y
Occupied during year	12	14	17	19	12	19	20	17	21	18	17
Occupied during last 6 years	12	16	21	21	21	22	23	23	23	23	23

Supplementary BMU											
Salish Connectivity Area	Y	Y	Y	Y	N	Y	Y	Y	Y	Y	Y
Flathead Valley	Y	N	Y	Y	Y	Y	Y	Y	Y	Y	Y
Flathead Reservation	N	N	Y	Y	Y	Y	Y	Y	Y	Y	Y
Ninemile Connectivity Area	N	N	N	N	N	N	N	N	N	Y	N
South End	N	Y	N	Y	N	N	Y	Y	Y	Y	Y
East Front	Y	Y	Y	Y	Y	Y	Y	Y	Y	N	N
Blackfeet Reservation	Y	Y	Y	Y	Y	Y	Y	N	N	Y	Y
Occupied during year	4	4	5	6	4	5	6	5	5	6	5
Occupied during last 6 years	4	5	6	6	6	6	6	6	6	7	7
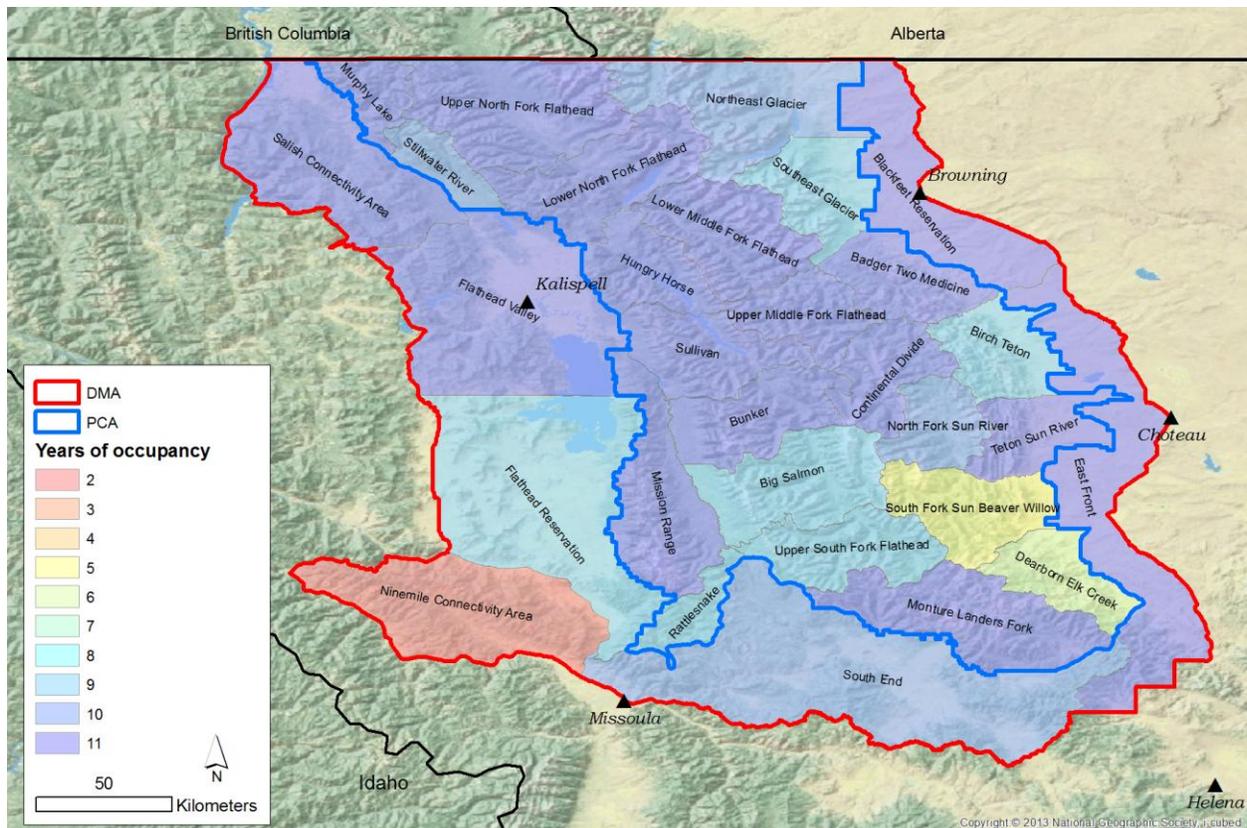
Figure 4.1.1. Summed years of occupancy of BMUs (PCA) and supplementary BMUs (Zone 1 of DMA) by female grizzly bears with young (cubs, yearlings, or 2-year-olds), as defined as occupancy during at least 1 year during the last 6 years, NCDE, 2004–2014.

reproductive females annually. Using a 6-year running tally, the demographic standard of 21 of 23 BMUs occupied was met each year beginning in 2006, 3 years prior to the time the full 6 years of radio-telemetry monitoring was realized (Figure 4.1.2). Using the 6-year running tally, the demographic standard of no two adjacent BMUs unoccupied was met each year beginning in 2009, concurrent with the year when the full 6 years of monitoring was realized. During the most recent 6-year period (2009–2014), all 23 BMUs were occupied by females with young during at least 1 of the 6 years.

During 2004–2014, all 7 supplementary BMUs were occupied by reproductive females during at least 1 year (Table 4.1.1). On average, at least 5 of 7 (71%) supplementary BMUs were occupied per year. Using a 6-year running tally, 6 of 7 (86%) supplementary BMUs were occupied by 2006, and no two adjacent supplementary BMUs were unoccupied starting in 2005 (Figure 4.1.3). During the most recent 6-year period (2009–2014), all 7 supplementary BMUs were occupied by females with young during at least 1 of the 6 years.
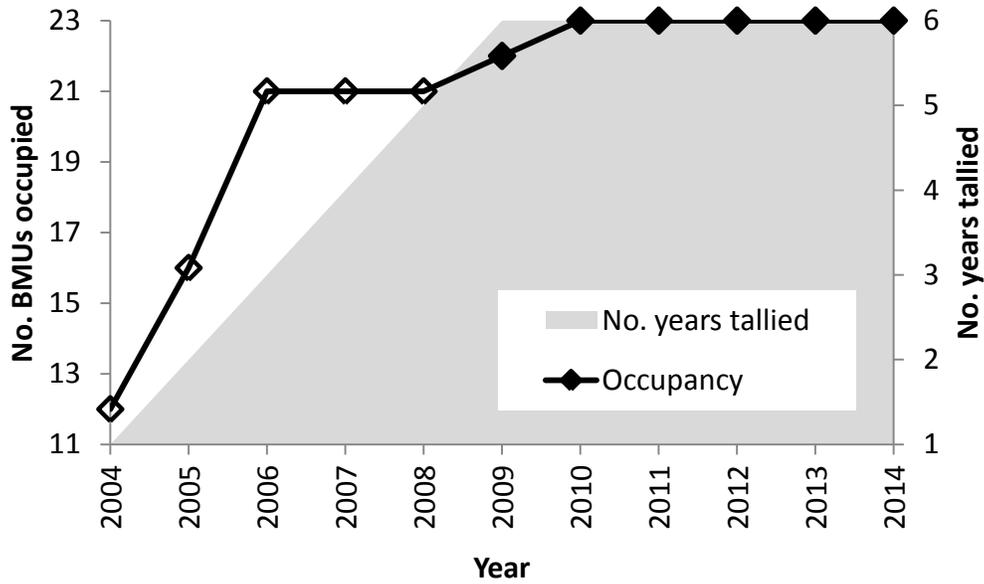
Figure 4.1.2. Number of BMUs occupied by female grizzly bears with young (cubs, yearlings, or 2-year-olds) at least once during the last 6 years, by year, NCDE, 2004–2014. Open symbols represent 6-year tallies when ≥2 adjacent BMUs were unoccupied; closed symbols represent when no adjacent BMUs were unoccupied. Radio-telemetry monitoring began in 2004, therefore the number of years tallied was <6 until 2009 when the first 6-year tally was realized.
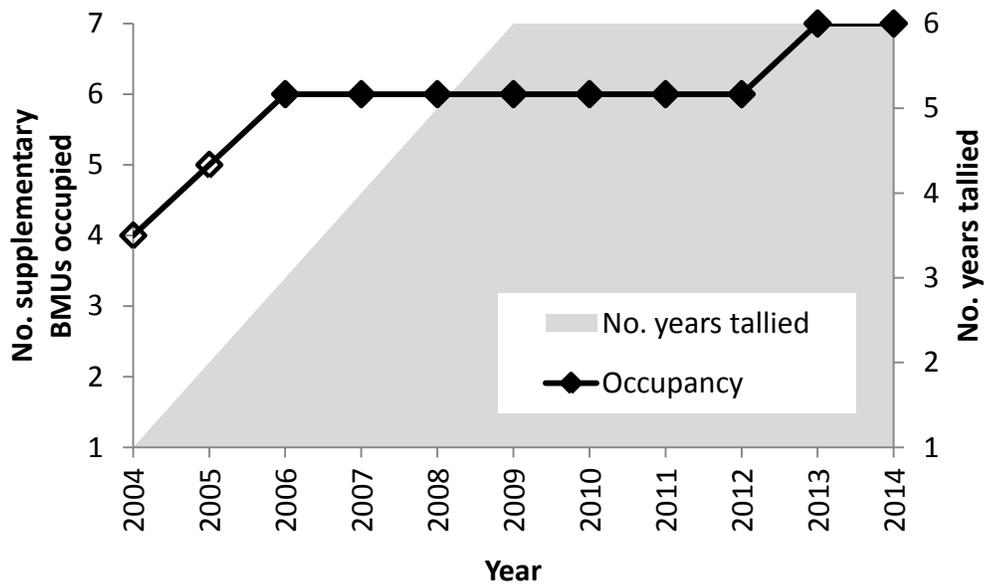
Figure 4.1.3. Number of supplementary BMUs occupied by female grizzly bears with young (cubs, yearlings, or 2-year-olds) at least once during the last 6 years, by year, NCDE, 2004–2014. Open symbols represent 6-year tallies when ≥2 adjacent subunits were unoccupied; closed symbols represent when no adjacent subunits were unoccupied. Radio-telemetry monitoring began in 2004, therefore the number of years tallied was <6 until 2009 when the first 6-year tally was realized.

4.2 Population Distribution

When the grizzly bear was listed as threatened in 1975, its distribution in the NCDE was likely confined to the PCA, and the Recovery Plan (1993) identified the PCA as the area of distribution in 1993. In 2002, a map of grizzly bear distribution was developed by bear researchers and managers for both the NCDE and CYE, based on female and cub monitoring data, nuisance bear activity information, radio-telemetry records, and credible observations from the previous 5–10 years (Wittinger 2002). By delineating the boundary between the NCDE and CYE by the Kootenai River (which coincides with the NCDE DMA boundary), the estimated area of grizzly bear distribution within the NCDE in 1992–2002 was 34,033 km^2, representing a 47% increase from the area of the PCA. Since that time, no further estimates of grizzly bear distribution have been developed for the NCDE.

Bjornlie et al. (2014) developed a technique to estimate grizzly bear distribution that would allow for use of all verified grizzly bear location data. Unlike the complex and time-consuming kernel estimators previously used to estimate grizzly bear distribution in the GYE, this method used zonal analysis and ordinary kriging to predict distribution, based on observed presence within a grid. The simplicity of this method allows bear distribution maps to be updated frequently. In this section, we utilized this method to estimate the current distribution of grizzly bears in the NCDE and compared that distribution to the PCA and the estimated distribution in 2002.

Methods

We used all verified grizzly bear locations from 2004–2014 to create a distribution map for the NCDE. Verified locations were collected from: GPS (Global Positioning System) transmitters; VHF telemetry flights; capture and mortality locations; grizzly bear-human conflict sites; observations (sighting or track) or remote camera photos that were confirmed by agency personnel; and opportunistic samples (hair, blood, scat, or tissue) that were confirmed grizzly bear by DNA analysis. We also used the location of hair samples collected in the USGS DNA projects from 2004-2011 (Kendall et al. 2009, USGS unpublished data).

We used the Geographic Information System (GIS) software ArcMap 10.1 (Environmental Systems Resource Institute, Redlands, CA) to place a 7 x 7 km grid over the area that contained all of the grizzly bear locations. The grid-cell size was based on the average daily movements from 31 male grizzly bears, wearing GPS transmitters from 2003-2012, located throughout the ecosystem. Our mean daily movement for male grizzly bears was 7.44 km (95% CI: 5.84–9.05 km). We used the ordinary kriging method used by Bjornlie et al. (2014) to perform our distribution analysis.

Results

Using all of the verified grizzly bear locations from 2004–2014 (n = 210,126) we estimated total distribution of grizzly bears to be 55,200 km^2. This represents a 62% increase from the estimated distribution during 1992–2002 (Wittinger 2002) and a 139% increase from the area of the PCA where bear distribution was estimated prior to 1993 (USFWS 1993). Although the methods differed, these estimates correspond with an increase of about 1,500 km^2 of occupied range per year. Current grizzly bear distribution extends beyond the DMA in all cardinal directions. Most notably, total distribution extends into approximately 14% (6,673 km^2) of Management Zone 3 and into approximately 9% (1,634 km^2) of Management Zone 2 (Figure 4.2.1), the area of connectivity with the GYE. Additionally, 100% of the Salish Connectivity Area (2,141 km^2) and 63% of the Ninemile Connectivity Area (1,314 km^2) lie within the current distribution of grizzly bears.
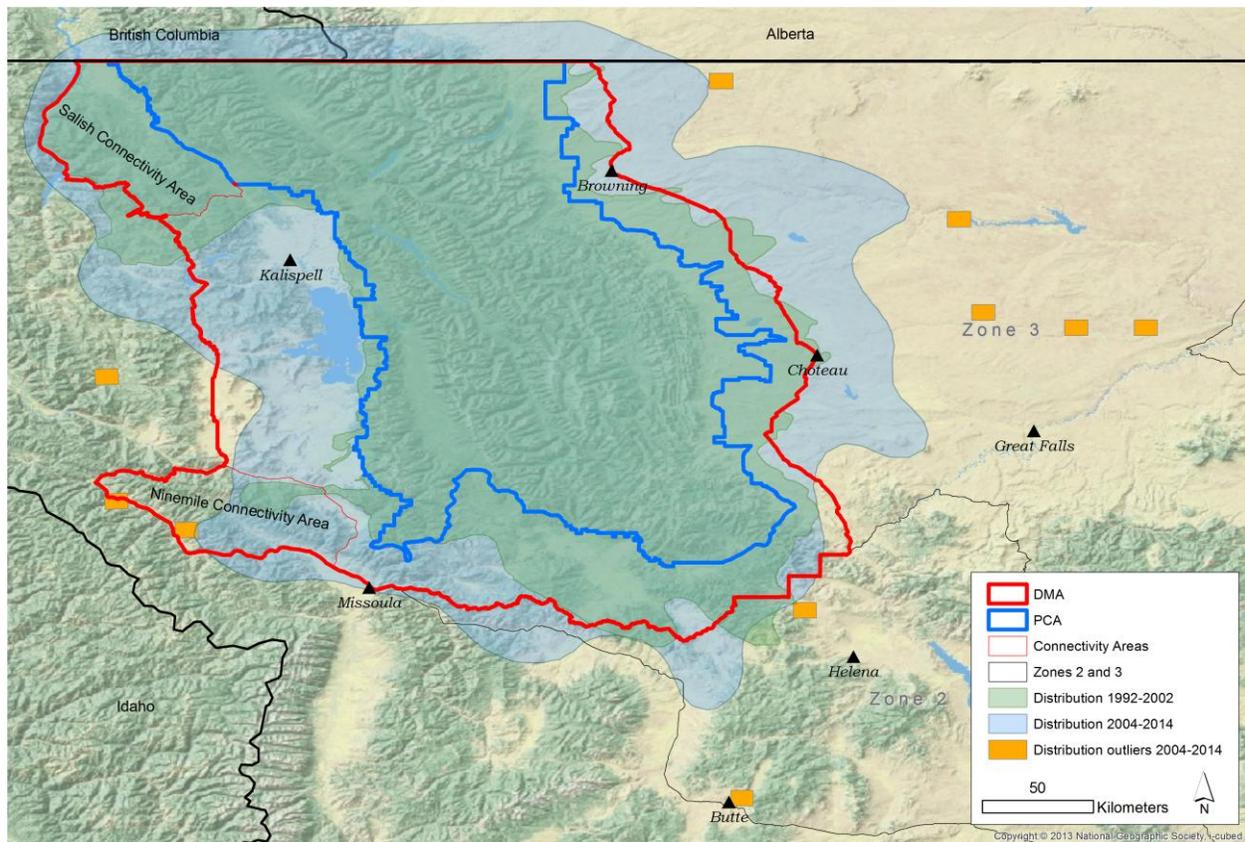
Figure 4.2.1. Estimated current distribution grizzly bears (blue shaded area) during 2004–2014, relative to the estimated distribution circa 1992–2002 (green shaded area), the PCA (blue line), and the DMA (red line). Orange cells represent outlying verified grizzly bear observations that occurred beyond the kriging surface.

4.3 Relative Population Density

The 2004 DNA mark/recapture estimate of Kendall et al. (2009) represents our only reliable estimate of the NCDE bear population size. Kendall et al. (2009) developed a relative density map for their sampling area, based on the average number of female and male grizzly bears detected per cell (Section 3). The map showed that DNA detections were greatest in the northern third of the PCA, particularly inside Glacier National Park. Points of detection, however, are not representative of the potential movements or home ranges of individuals. For example, while Kendall found that a significant proportion of detections occurred within Glacier National Park, the method did not always provide information about whether or not detected individuals also used areas outside of the park, especially when individuals were only detected once. In this section, we combined information about movements from GPS-collared bears with the information from DNA detections to refine the relative density map. Our goals were to estimate relative density within DMA subunits, and to determine the potential number of individuals that may have utilized each of the subunits during 2004. This information was used to evaluate the distribution of our radio-marked sample (Section 4.5).

Methods

We estimated the relative population density of male and female grizzly bears within the PCA and surrounding areas using the genetic detection data from Kendall et al. (2009) and movement data from bears fitted with GPS transmitters. We first used the geographic locations of individual grizzly bears genetically detected at hair traps within 7-km^2 grid cells in 2004. Although Kendall et al. (2009) collected hair at rub trees and hair traps, we included only hair-trap detections in our analysis, because hair traps were distributed systematically within and just outside the PCA. Kendall et al. (2009) sampled the population 4 times from June through August. We collapsed multiple locations of each individual into one coordinate representing the median detection location. Second, we used location data from our sample of GPS-collared bears to estimate typical movement patterns, which could be applied to the DNA-detected individuals. We screened the GPS data to include only those females and males for which we had ≥30 and ≥20 bear-days/year, respectively, during June–August to correspond with the genetic sampling period. The lower value corresponding with males was due to the smaller sample size of GPS-collared males available for analysis. We standardized the data by calculating a median coordinate for each bear-day, thus eliminating any differences in sample size related to fix interval. For each GPS-collared individual, we randomly selected one median daily location and calculated the distance to all other median daily locations for that same bear-year, with 10 repetitions of this process for each bear-year. Third, we summarized these inter-daily distances using percentiles (Table 4.3.1) and used the

information to assign the 'probability of use' for a series of distance buffers from the detection point, wherein the probability of a bear using an area declined with distance from its detection point (Table 4.3.1). Finally, we developed relative population density maps for male and female grizzly bears within and directly adjacent to the DMA, by summing the probabilities at the center points of 3-km^2 grid cells. We utilized this smaller grid cell size, because the original 7-km^2 grid cells were relatively large compared to the width of the distance buffers. We extended our density analysis outside of the exterior boundary of the area genetically sampled in 2004 to account for the potential movement probabilities for bears detected near the edge, extended both male and female grids to approximately the 95th distance percentile (corresponding to 0.05 probability of use). Relative density estimates were standardized among cells to range from 0–1 for each sex.

Results

Our density maps and population projections were based on geographic distribution of 266 females and 182 males that were detected at hair traps in 2004 (Kendall et al. 2009). Movement parameters applied to these detections were based on GPS locations obtained during 83 bear-years for females and 37 bear-years for males. Movements of GPS-collared grizzly bears during the June–August sampling period varied by sex (Table 4.3.1). We estimated that individual female and male bears had a 0.50 probability of using areas 6.1 and 13.4 km from their detection point, respectively. We estimated that they had only a 0.05 probability of using areas 19.6 and 56.7 km from their detection point, respectively.

Table 4.3.1. Estimated probability that female and male grizzly bears utilize areas at variable distances from their median DNA detection points during June–August. Estimates were based on percentiles of inter-daily distances randomly sampled from GPS-collared bears monitored during the same months. A series of buffers were applied to DNA detection points at the distances described and assigned corresponding probabilities.

Percentile	Estimated probability	Distance (km)	
		Female	Male
10th	0.90	1.59	2.29
20th	0.80	2.81	4.86
30th	0.70	3.85	7.38
40th	0.60	4.95	10.29
50th	0.50	6.10	13.44
60th	0.40	7.49	17.99
70th	0.30	9.21	24.67
80th	0.20	11.63	31.38
90th	0.10	15.67	45.43
95th	0.05	19.64	56.66

Our spatial analysis indicated the relative densities of both females and males were greatest within Glacier National Park, and generally declined from north to south (Figures. 4.3.1 and 4.3.2). Localized areas of relatively high female densities were observed in most DMA subunits. The application of much larger movement buffers for detected male bears served to smooth their relative density to a larger degree than females. Thus, male densities radiated outward from the center of Glacier National Park. Averaging relative density within DMA subunits, estimated female densities were ≥2 times greater and male densities were ≥1.5 times greater in Glacier National Park than in any other subunit. Densities were also relatively high in the Middle Fork Flathead River, North Fork Flathead River, and South Fork Flathead River-Swan Valley subunits (Table 4.3.2). Local densities were also relatively high along the Rocky Mountain Front in the Blackfeet Reservation and East Front subunits, especially among males.

Although Glacier National Park had the highest proportion of DNA detections and highest relative densities, many of the bears detected there likely utilized other DMA subunits and/or southern Canada. Based on the median inter-daily movement rates, we estimated 34% of detected females and 73% of detected males had a ≥0.50 probability of using more than one DMA subunit or included Canada or Zone 3 in their movements. Accounting for their most distant potential movements (corresponding with a 0.05 probability of use), we estimated that 94% of females and 100% of males utilized more than one subunit. For example, 41% of detected females were detected within Glacier National Park and thus were known to use it with a probability of 1.00. But, based on their median detection location and likely movement distances, we estimated that another 8% of females likely used the Park (with ≥0.50 probability), and another 16% possibly used the Park (with probability of 0.05; Table 4.3.3). Extrapolating those proportions to the total estimated population in 2004 (Kendall et al. 2009), we estimate that 191 females used the Park, 231 used the Park with a 0.50 probability, and 306 used the Park with a 0.05 probability. Similar proportions and numbers were calculated for other DMA subunits, Canada, and Zone 3. It is important to note that these estimated proportions and numbers only pertain to the 2004 population estimate, as sampled primarily within the PCA. Additional grizzly bears that may have resided outside of the sampling area would have been underrepresented in the population estimate and in this analysis of relative density. In addition, with the positive population growth the NCDE grizzly bear population likely experienced since 2004, these estimates of relative density may not be applicable to current population status.
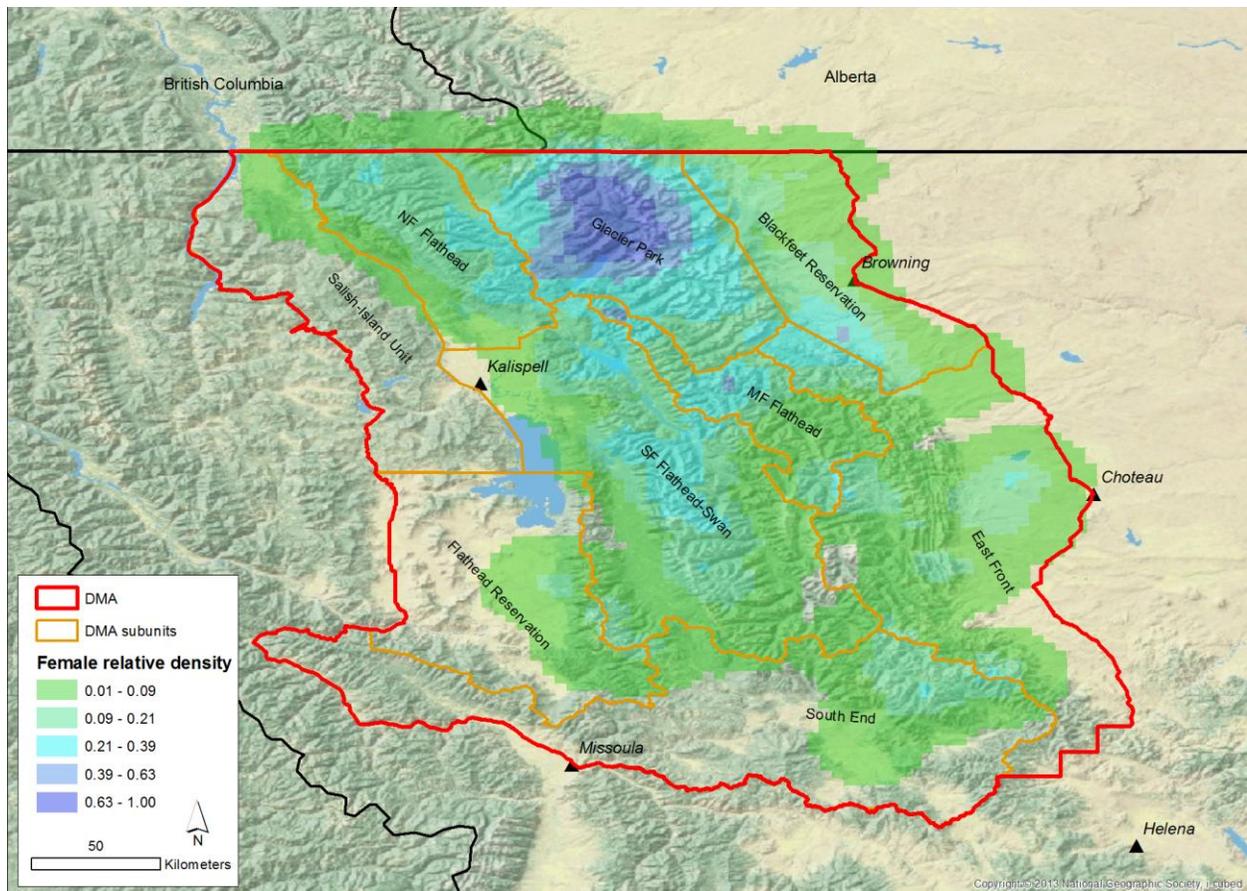
Figure 4.3.1. Estimated relative female grizzly bear population density (all age classes), relative to DMA subunits, NCDE, 2004. Analysis involved only those females detected at hair traps uniformly distributed throughout the NCDE. A series of distance buffers were applied to the median detection point for each individual and assigned corresponding probability for use, wherein the probability of a bear using an area declined with distance from its detection point. Probabilities were summed at the midpoints of 3-km^2 cells and standardized to range from 0 to 1. Due to potential movement patterns, relative density was estimated outside of the DNA sampling area, but density estimates do not account for additional bears that were potentially present outside of the genetic sampling area.
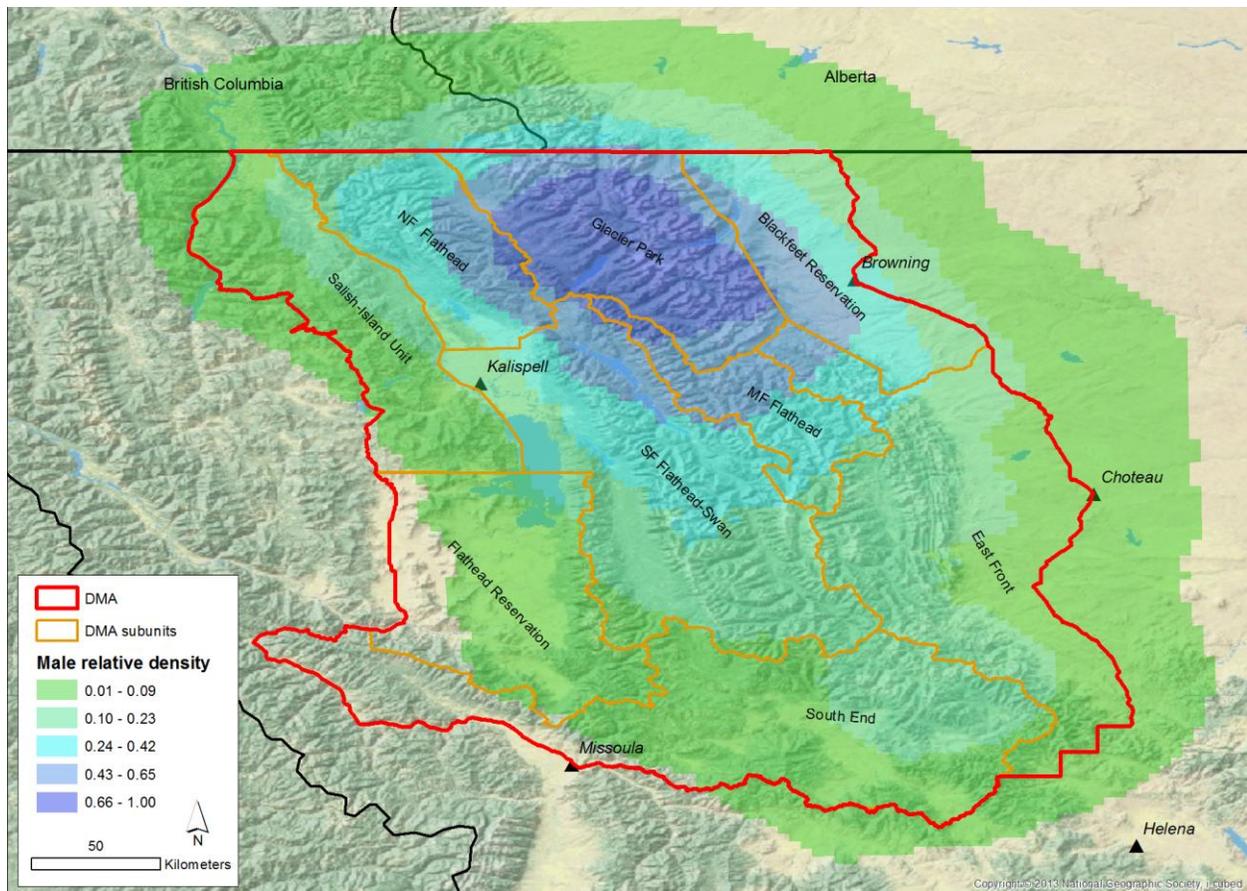
Figure 4.3.2. Estimated relative male grizzly bear population density (all age classes), relative to DMA subunits, NCDE, 2004. Analysis involved only those males detected at hair traps uniformly distributed throughout the NCDE. A series of distance buffers were applied to the median detection point for each individual and assigned corresponding probability for use, wherein the probability of a bear using an area declined with distance from its detection point. Probabilities were summed at the midpoints of 3-km2 cells and standardized to range from 0 to 1. Due to potential movement patterns, relative density was estimated outside of the DNA sampling area, but density estimates do not account for additional bears that were potentially present outside of the genetic sampling area.

Table 4.3.2. Mean relative density of female and male grizzly bears within DMA subunits, 2004. Relative density estimates were standardized for each sex, thus mean density estimates were calculated with cell values ranging from 0 to 1.

	Cells with >0 summed probability[a]		All cells in subunit[b]	
	Female	Male	Female	Male
Glacier National Park[c]	0.44	0.82	0.44	0.82
Middle Fork Flathead River[c]	0.20	0.55	0.20	0.55
North Fork Flathead River[d]	0.18	0.48	0.18	0.48
South Fork Flathead River-Swan Valley[d]	0.13	0.28	0.12	0.28
East Front[d]	0.09	0.17	0.07	0.17
Blackfeet Reservation[d]	0.13	0.25	0.07	0.24
South End[d]	0.07	0.08	0.02	0.07
Flathead Reservation[d]	0.05	0.04	0.01	0.03
Salish-Island Unit[d]	0.06	0.11	0.01	0.11

[a] Mean density accounting only for cells where movement buffers for ≥1 bear were estimated.
[b] Mean density accounting for all cells in the subunit, irrespective of bear distribution.
[c] Subunit was fully sampled and fully occupied, thus the two estimates were equivalent.
[d] Subunit was not fully sampled and/or occupied, thus the two estimates may differ.

Table 4.3.3. Estimated proportion of female and male grizzly bears detected by hair traps in 2004 (Kendall et al. 2009) that may have used DMA subunits, Canada, and Zone 3 with estimated probabilities of 1.00, 0.50, and 0.05. Probabilities of use were estimated based on movement rates of GPS-collared grizzly bears. Extrapolated numbers of bears are in parentheses, based on an estimated population size of 765 (471 females and 294 males).

| | Proportion of detected individuals (extrapolated number of individuals) | | | | | |
| | 1.00 probability of use[a] (from DNA detections) | | ≥0.50 probability of use[b] (from median inter-daily movement rate) | | 0.05 probability of use[b] (from 95th percentile of inter-daily movement rate) | |
DMA subunit (or other area)	Female	Male	Female	Male	Female	Male
Glacier National Park	0.41 (191)	0.38 (113)	0.49 (231)	0.57 (168)	0.65 (306)	0.84 (247)
South Fork Flathead River-Swan Valley	0.17 (78)	0.17 (50)	0.23 (108)	0.29 (85)	0.41 (193)	0.94 (276)
Blackfeet Reservation	0.09 (44)	0.12 (36)	0.12 (57)	0.24 (71)	0.60 (283)	0.71 (209)
North Fork Flathead River	0.10 (46)	0.11 (32)	0.14 (66)	0.20 (59)	0.26 (122)	0.63 (185)
East Front	0.11 (51)	0.09 (27)	0.17 (80)	0.25 (74)	0.26 (122)	0.66 (194)
Middle Fork Flathead River	0.08 (35)	0.07 (21)	0.14 (66)	0.23 (68)	0.35 (165)	0.86 (253)
South End	0.04 (18)	0.04 (11)	0.06 (28)	0.08 (24)	0.09 (42)	0.17 (50)
Flathead Reservation	0.02 (7)	0.01 (2)	0.03 (14)	0.02 (6)	0.05 (24)	0.22 (65)
Salish-Island	0	0	0.01 (5)	0.04 (13)	0.06 (28)	0.46 (134)
Canada	0	0	0.04 (11)	0.08 (15)	0.18 (85)	0.52 (153)
Zone 3	0	0.01 (2)	<0.01 (3)	0.04 (7)	0.09 (42)	0.81 (238)

[a] In these columns, proportions sum to 1.00 and numbers sum to 471 for females and 294 for males (765 total), because each individual's median detection point was located in only one subunit.

[b] In these columns, proportions sum to >1.00 and numbers sum to >765, because distance buffers for some individuals were located within ≥1 subunit.

4.4 Documented and Estimated Mortality

Documenting the number of mortalities has long been a part of monitoring the status and trend of the NCDE grizzly bear population. An interagency grizzly bear mortality database for the NCDE was established in 1967 by MFWP and is currently maintained cooperatively through state, federal, and tribal wildlife agencies. These data have been used to evaluate number of documented mortalities relative to mortality limits set down in the code of federal regulations in 1975 (i.e., annual human-caused mortalities not to exceed 25; see Dood and Pac 1993) and, more recently, those established in the Recovery Plan (i.e., annual human-caused mortality not to exceed 4% of the estimated population size; USFWS 1993).

While information on documented mortalities can be and has been vital for meeting recovery goals, it is recognized that an unknown number of additional mortalities occur each year that are not discovered or reported to management authorities and are thus not a part of the official record (Brannon et al. 1988, McLellan et al. 1999). It is important that these unreported mortalities be incorporated into estimation of sustainable mortality, especially as predicted from survival rates and estimated population size. Using data from radio-marked bears monitored during 1975–1986, Brannon et al. (1988) estimated that 2.9% of annual mortalities of grizzly bears in the NCDE were unreported. Within 13 study areas in Alberta, British Columbia, Montana, Idaho, and Washington, McLellan et al. (1999) estimated that only about half (46–51%) of grizzly bear mortalities were reported during 1975–1997. Cherry et al. (2002) developed a method for estimating the annual number of unreported mortalities, and this method has been utilized to estimate annual mortality of grizzly bears in the GYE since 2007 (IGBST 2007). Here, we utilize the Cherry et al. (2002) method to estimate the total number of annual mortalities of independent (≥2 years old) bears from all causes of death that occurred during 2004–2014 inside the DMA, and investigate patterns in the causes of death.

Methods

Our goal was to estimate the total number of mortalities of independent female and male grizzly bears that occurred inside the DMA each year during 2004–2014. Mortalities were classified using the definitions for cause, certainty, and method of discovery as described in Cherry et al. (2002; Table 4.4.1). Most records in the mortality database included: known or estimated date of death; sex; age or estimated age class; known or suspected cause of death; location of death; and other pertinent information. In some cases, such as when only parts of a decomposed carcass were found, some of these data were lacking. For those mortalities where sex and/or age of the individual were unknown, we randomly assigned a sex and/or an age class (dependent/independent) by the flip of a coin, and these designations became part of

Table 4.4.1. Terms and definitions used to classify mortalities of independent (≥2 years old) grizzly bears in the NCDE, 2004–2014.

Category	Definition
Certainty of mortality	Known: a carcass or parts of a carcass found to substantiate death.
	Probable: strong evidence to indicate mortality, but no carcass recovered. Includes cases where evidence indicated severe wounding and blood loss, and/or observations suggest the bear displayed abnormal behavior after the encounter.
	Possible: some presumptive evidence of mortality, but no prospects for validation. Includes defense-of-life situations where shots were fired, but no evidence of significant wounding was found. Includes hearsay evidence of poaching or malicious death.
Method of discovery	Agency removal: death of bear documented because of sanctioned removal by agency (100% reporting rate).
	Telemetry: death of bear wearing functional transmitter documented through telemetry (100% reporting rate).
	Reported: death of bear not wearing functional radio-transmitter documented through public report to state or federal agency or agency discovery (<100% reporting).
Cause of mortality	Defense of life: bear legally killed by person while defending their life.
	Illegal defense of property: bear illegally killed by the public while defending property.
	Illegal hunting (misidentified): bear mistaken for black bear and illegally harvested during a sanctioned black bear hunting season.
	Agency removal: bear legally killed or removed because of management action, or live bear legally moved from NCDE to other ecosystems for augmentation of population, or unintended death of bear due to capture and/or immobilization.
	Natural: positively or reasonably attributed to natural cause.
	Poaching/malicious kill: an illegal mortality perpetrated by the public.
	Train collision: bear killed by train.
	Undetermined: cause could not be determined.
	Vehicle collision: bear killed by motor vehicle.

the permanent record. To obtain a total number of independent mortalities for each sex, we classified mortalities into three groups: (1) agency-sanctioned management removals; (2) known or probable deaths of bears wearing functional radio-transmitters (excluding agency removals); and (3) mortalities of non-radioed bears reported by the public or discovered by agency personnel. Management removals and deaths of radio-marked bears were well documented and annual counts were considered censuses. Annual counts of mortalities of non-radioed bears represent some unknown fraction of the true number

and could not be considered censuses. Therefore, we used the method of Cherry et al. (2002) to inflate this count to an estimate of the sum of reported and unreported mortality of non-radioed bears. This method utilized information from documented deaths of radio-marked individuals. As with unmarked bears, the public reported some deaths of radio-marked bears, and this reporting rate provided the basis for analysis. To maximize our sample for this analysis, we included known and probable deaths of grizzly bears that occurred while they were wearing functional radio-transmitters during 1990–2014. This sample included individuals captured and radio-marked for both research and management purposes. We excluded radio-marked bears that died as a result of management removals, as we assumed a 100% reporting rate for this cause of death. Each death of a radio-marked bear was classified as being either reported or unreported. We defined a reported death as one where a dead bear was reported to a wildlife management agency (state or federal) without the aid of radio-telemetry, including: those reported to management authorities after being either discovered or killed by the public; those discovered by employees of state, federal, or tribal agencies; and bears killed by train collisions and reported by Burlington Northern personnel. We defined an unreported death as the death of a bear discovered exclusively by radio-telemetry. The numbers of reported and unreported deaths of radio-marked bears, both sexes combined, were used to estimate a reporting rate. This rate, expressed as a beta distribution, was then used as a prior distribution in a Bayesian analysis to estimate the total number of reported and unreported deaths of non-radioed bears, as a function of the number of reported deaths of non-radioed bears for each sex (Cherry et al. 2002). We used the median of the posterior distribution to obtain a point estimate of the number of total deaths relative to the number of reported deaths (IGBST 2005). Thus, the final estimated number of annual mortalities was a sum of: (1) management removals; (2) radio-marked losses; and (3) estimated total reported and unreported losses of non-radioed bears.

We summarized cause of death for documented mortalities during 2004–2014 and mapped their locations by DMA subunit and presence inside or outside the PCA and the DMA, using ArcMap 10.1 software (Environmental Systems Resource Institute, Redlands, CA). Spatial summaries of mortalities excluded estimated unreported mortalities, as these mortalities lacked any location information. We did, however, extrapolate cause of death within our estimate of total mortality, based on reporting rates and cause-of-death frequencies among the radio-collared sample (1990–2014).

Results

We obtained records of 66 radio-marked grizzly bears (39 female: 27 male) that died between 1990 and 2014. Three of these deaths (5%) occurred outside of the DMA. Overall, 44% of radio-marked deaths were reported, providing a ratio of unreported to reported mortality of 1.27:1.00. Reporting rate varied by cause of death (Table 4.4.2). Reporting rates were relatively high (0.67–1.00) for defense-of-

Table 4.4.2. Observed reporting rate, by cause of death, among documented known or probable mortalities of radio-marked, independent (≥2 years old) grizzly bears, NCDE, 1990–2014. Agency removals were excluded from this sample, because reporting rate was assumed to be 1.00. The sample was used for the Bayesian estimate of total number of reported and unreported deaths of non-radioed bears, predicted from the number of reported deaths of non-radioed bears (Cherry et al. 2002).

| Cause of death | n | Reporting of Mortality | | Proportion reported | Reporting rate category |
		Public (reported)	Telemetry (unreported)		
Poaching/ malicious kill	21	4	17	0.19	Low
Undetermined	11	2	9	0.18	Low
Illegal defense of property	9	6	3	0.67	High
Natural	7	0	7	0.00	Low
Defense of life	6	6	0	1.00	High
Train collision	6	5	1	0.83	High
Automobile collision	4	4	0	1.00	High
Illegal hunting (misidentification)	2	2	0	1.00	High
Combined	66	29	37	0.44	

Table 4.4.3. Bayesian estimates of the total number of reported and unreported deaths of non-radioed bears, predicted from the number of reported deaths of non-radioed bears in the high- and low-reporting rate categories (Cherry et al. 2002). Estimate was based on the ratio of unreported to reported deaths among 66 radio-marked bears (27 in high-reporting and 39 in low-reporting categories), NCDE, 1990-2014.

| Number of reported deaths/year | Estimated sum of reported and unreported deaths/year | |
	High reporting rate	Low reporting rate
0	1	1
1	1	4
2	2	10
3	3	16
4	5	22
5	6	28
6	7	34
7	8	40
8	9	47
9	11	53
10	12	59
11	13	65
12	14	71
13	15	77
14	17	83
15	18	89

property and defense-of-life situations, train and automobile collisions, and bears mistakenly killed by black bear hunters. Conversely, reporting rates were relatively low (0–0.19) for poaching/malicious kills, natural mortalities, and deaths from undetermined causes. Reporting rate differed between these two groups ($\chi^2 = 31.6$, P < 0.001). Summed for the high-reporting categories, 85% of deaths were reported, providing a ratio of unreported to reported mortality of 0.17:1.00. Summed for the low-reporting categories, 15% of deaths were reported, providing a ratio of unreported to reported mortality of 5.50:1.00. Ratios of Bayesian estimates of the sum of reported and unreported deaths, predicted from the number of reported deaths each year, are given in Table 4.4.3. These estimates were applied separately to each sex.

We documented 169 (77 F, 89 M) known or probable mortalities of independent grizzly bears within the DMA during 2004–2014. This count included 4 unknown-age/unknown-sex bears randomly assigned as independent bears (2 F, 3 M) and 6 independent unknown-sex bears randomly assigned for sex only (1F, 3 M). Inflating this estimate using the Bayesian method, our estimate of total mortalities within the DMA was 338 for the study period or a mean of 30.7 total, 13.8 female, and 16.9 male mortalities/year (Table 4.4.4). There appeared to be a slight increasing trend in the estimated total mortalities, consistent with an increase of approximately 2–3%/year, however this temporal trend was not significant (P = 0.39; Figure 4.4.1). The percentage of documented mortalities that occurred outside of the PCA increased over the period (P = 0.07), with a linear trend that doubled from approximately 18% in 2004 to 44% in 2014 (Figure 4.4.2).

We documented an additional 18 (5 F, 13 M) known or probable independent mortalities that occurred outside of the DMA during this period or a mean of 1.6 total, 0.5 female, and 1.2 male mortalities/year. Only 9.6% (18 of 187) of documented mortalities occurred outside the DMA. Most of the mortalities that occurred outside the DMA were relatively close to the boundary, but the furthest was approximately 102 km east of the DMA boundary. Forty-four percent of the mortalities outside the DMA involved previously marked or radio-marked bears that were known to utilize areas inside the DMA.

Among documented independent mortalities, the leading cause of death was agency removal (Table 4.4.5). It should be noted that this cause also included bears removed and translocated for augmentation of the CYE population ($n = 10$) and bears that died from capture-related mortalities ($n = 5$). Other leading causes of mortality were poaching/malicious kills and defense of life kills. Extrapolating cause of death among the estimated number of total mortalities, proportions differed from documented mortalities due to differences in reporting rates. For example, because agency removals had a 100% reporting rate, this cause of death was estimated to account for only 0.16 of the 339 estimated total

Table 4.4.4. Summary of independent (≥2 years old) grizzly bear mortalities within the DMA, NCDE, 2004-2014.

| Sex | Year | Documented mortalities by method of discovery | | | | Estimated reported and unreported[e] (C) | Estimated total mortality (A + B + C) |
		Agency removal[a] (A)	Telemetry[b] (B)	Reported[c] (high)	Reported[d] (low)		
Female	2004	2	4	2	2	12	18
	2005	5	1	0	1	5	11
	2006	1	2	0	0	2	5
	2007	0	0	5	2	16	16
	2008	3	0	2	1	6	9
	2009	1	2	2	1	6	9
	2010	2	1	1	1	5	8
	2011	3	0	6	1	11	14
	2012	0	0	2	1	6	6
	2013	3	1	4	2	15	19
	2014	3	0	5	5	34	37
	Total	23	11	29	14	118	152
	Mean	2.1	1.0	2.6	1.3	10.7	13.8
Male	2004	1	0	4	1	9	10
	2005	1	1	4	4	27	29
	2006	3	2	0	1	11	16
	2007	2	1	6	3	23	26
	2008	1	0	2	1	6	7
	2009	1	0	4	3	21	22
	2010	4	0	1	1	5	9
	2011	7	0	3	1	7	14
	2012	5	0	7	1	12	17
	2013	5	2	0	3	17	24
	2014	1	0	0	2	11	12
	Total	31	6	31	21	149	186
	Mean	2.8	0.5	2.8	1.9	13.5	16.9

[a] Count of agency-sanctioned removals, including those involving radio-marked bears.

[b] Count of deaths for bears wearing functional radio-transmitters, except for agency removals.

[c] Count of non-radioed bear deaths reported by the public or discovered by agency personnel with high reporting rates (illegal defense-of-property, defense-of-life, train collision, automobile collisions, illegal hunting-misidentification).

[d] Count of non-radioed bear deaths reported by the public or discovered by agency personnel with low reporting rates (poaching/malicious, natural, undetermined).

[e] Bayesian estimate of the total number of reported and unreported deaths of non-radioed bears, predicted from the number of reported deaths of non-radioed bears in the high- and low-reporting rate categories (as per Cherry et al. 2002).
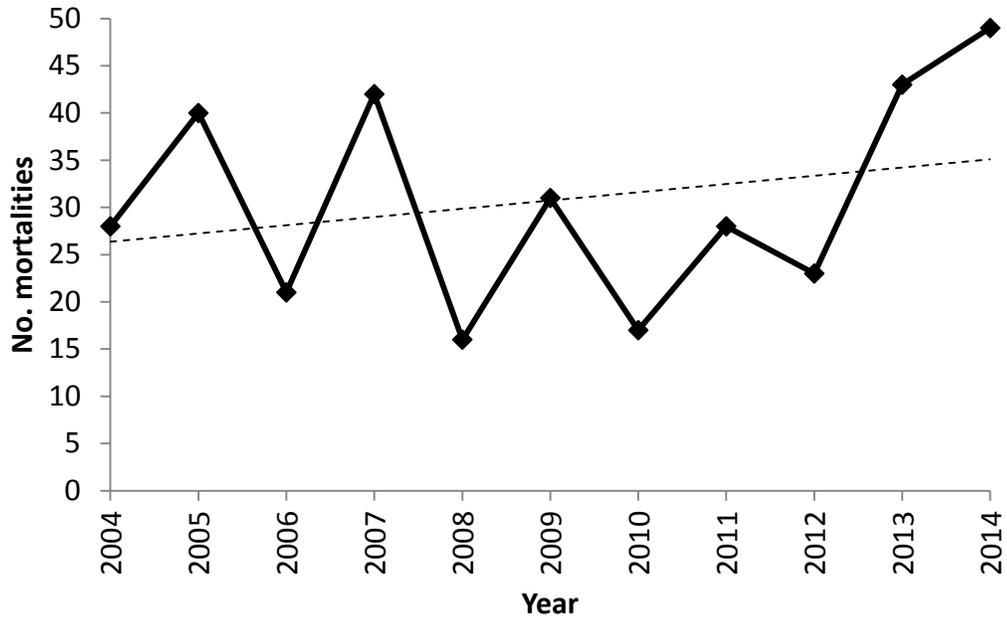
Figure 4.4.1. Total estimated number of independent (≥2 years old) grizzly bear mortalities within the DMA, by year, NCDE, 2004–2014.   The linear temporal trend in estimated numbers of mortalities was consistent with an increase of 2.9%/year, however it was not significant (P = 0.38).
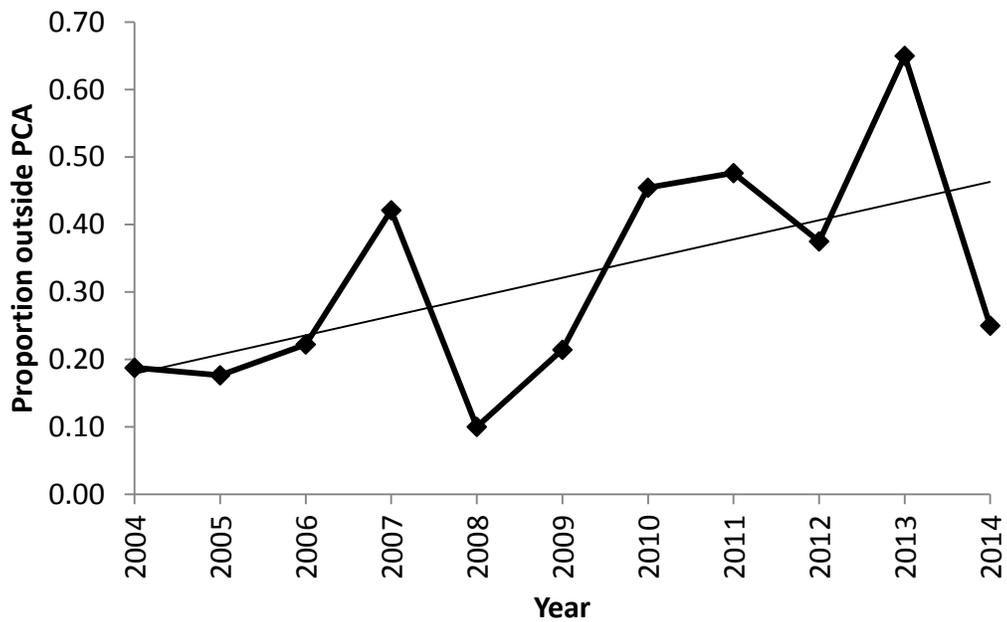
Figure 4.4.2. Proportion of documented independent (≥2 years old) grizzly bear mortalities that occurred outside of the PCA for the NCDE, 2004–2014. The linear temporal trend (P = 0.07) increased from 0.18 to 0.44 during the period.

mortalities, compared to 0.32 of the 169 documented mortalities. Conversely, because reporting rates for poaching/malicious kills and natural mortalities were low, these causes of death were estimated to account for higher proportions of the estimated total mortalities (0.32 and 0.12, respectively) compared to documented mortalities (0.18 and 0.04, respectively). For nearly all causes of death, we found that our extrapolated proportions were more similar to proportions observed among deaths of radio-marked bears during 1990–2014, compared to observed proportions among documented mortalities (Table 4.4.5).

By DMA subunit, the most documented independent mortalities occurred within the South Fork Flathead River-Swan Valley subunit (34%), while the fewest occurred within Glacier National Park (3%; Figures 4.4.3 and 4.4.4). Most of the mortalities in the South Fork Flathead River-Swan Valley subunit were concentrated in the Flathead and Swan River valleys. Vehicle collisions were the leading cause of death (27.3%) for grizzly bears in the South End subunit, while defense-of-life mortalities were relatively high in the East Front subunit. Illegal defense of property kill was a frequent cause of death outside the DMA.

Table 4.4.5. Proportional causes of death among independent (≥2 years old) grizzly bears in the NCDE: as observed among documented mortalities inside the DMA during 2004–2014; as extrapolated among total estimated number of mortalities inside the DMA during 2004–2014; and as observed among deaths of radio-marked bears during 1990–2014.

Cause	Documented (n = 169)	Estimated (n = 339[b])	Radio-marked (n = 79)
Agency removal[a]	0.32	0.16	0.16
Poaching or malicious kill	0.18	0.32	0.27
Defense of life	0.11	0.06	0.08
Undetermined	0.10	0.17	0.14
Train collision	0.08	0.06	0.08
Vehicle collision	0.08	0.04	0.05
Illegal hunting (misidentification)	0.06	0.03	0.02
Illegal defense of property	0.04	0.04	0.11
Natural	0.04	0.12	0.09

[a] In addition to bears removed due to human conflicts, proportion also includes bears removed for augmentation to CYE population and bears that died from capture-related causes.

[b] Bayesian estimate of the total number of reported and unreported deaths of non-radioed bears, predicted from the number of reported deaths of non-radioed bears in the high- and low-reporting rate categories (as per Cherry et al. 2002). Cause of death for unreported deaths was extrapolated from proportions of unreported deaths among radio-marked bears.
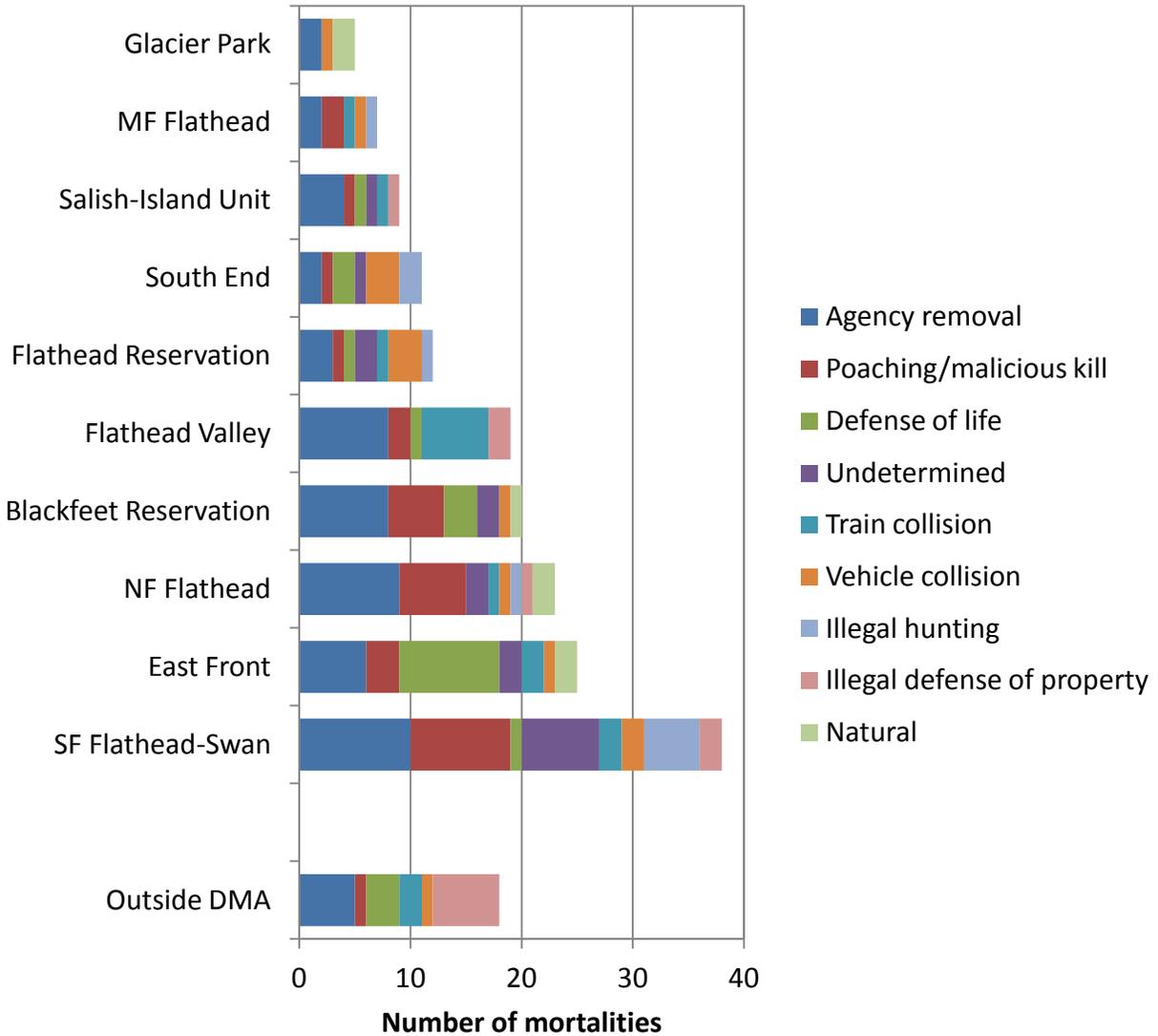
Figure 4.4.3. Number of documented mortalities of independent (≥2 years old) grizzly bears, by DMA subunits and cause of death, NCDE, 2004–2014.
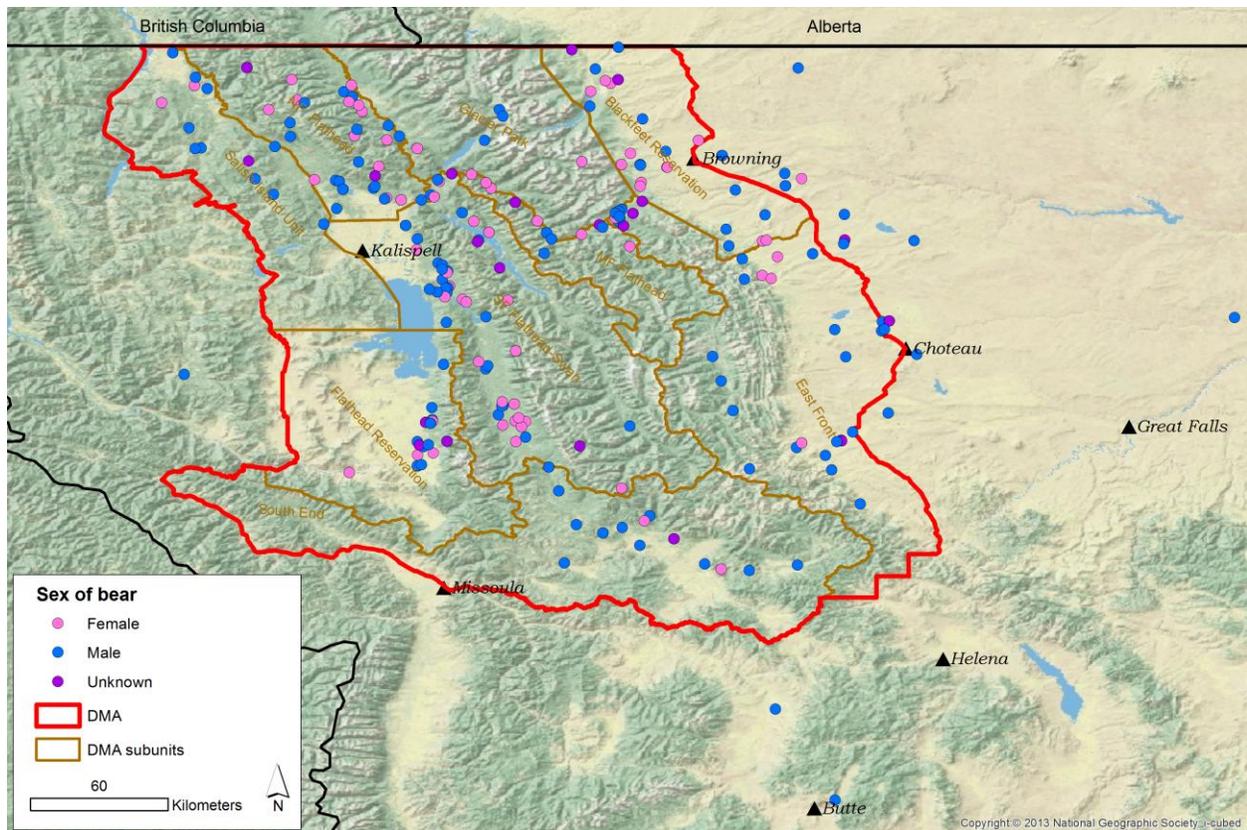
Figure 4.4.4. Spatial distribution of documented independent (≥2 years old) grizzly bear mortalities within (red dots) and outside (yellow) the DMA (red line), 2004-2014. Numbers represent the mean annual percent of all mortalities within the DMA occurring within each DMA subunit.

4.5 Demographic Monitoring: Independent Bear Survival

The Grizzly Bear Recovery Plan (1993) identified sightings of females with cubs as a method to estimate minimum population size, and a methodology utilizing observations of unduplicated females with cubs has been used to monitor the size and trend of the GYE grizzly bear population (Knight et al. 1995, IGBST 2012). However, the Recovery Plan (1993) also recognized that "because of the forested nature of much of the NCDE…the calculated minimum number of females with cubs will underestimate the actual number [population size]." Due to this limitation, an interagency team was established by state, federal, and tribal officials to monitor the survival and reproductive rates of radio-marked female grizzly bears from which population trend could be estimated. Since 2004, radio-telemetry monitoring of population vital rates (e.g., survival and fecundity) has been the primary tool for monitoring population trend.

In this section, we report estimates of survival for independent grizzly bears in the NCDE during 2004–2013. The DMA, representing the principal range of grizzly bears in the NCDE, is where demographic monitoring occurred and where annual estimates of total mortality were generated. While enumerating annual mortalities within this boundary can be accomplished with little difficulty (Section 4.4), it is not entirely possible to confine radio-telemetry monitoring of a live sample within the DMA, as bears residing near the edge commonly leave and reenter the area. Nonetheless, by capturing bears within the DMA and distributing our sample roughly in proportion to 2004 estimates of relative grizzly bear density across the study area (Kendall et al. 2009), our methods were designed to obtain a radio-marked sample representative of this core segment of the NCDE population. Vital rates estimated for this sample should be consistent with our estimates of total mortality within the DMA. Therefore, an additional goal of this section was to examine the spatial distribution of the radio-marked sample and evaluate its representation of the population within DMA.

Methods

Field Methods

We captured grizzly bears primarily using leg-hold snares and culvert traps, following the handling and immobilization procedures found in the MTFWP Institutional Animal Care and Use Committee protocols for grizzly bears and black bears (MTFWP 2004). We tagged all bears subcutaneously with microchips for identification (American Veterinary Identification Devices, Inc. [AVID], Norco, CA). We pulled a vestigial premolar tooth for cementum annuli age determination (Stoneberg and Jonkel 1966; performed by Mattson's Lab) and/or estimated age based on body size and

tooth eruption, wear, and staining. We fit most independent (≥2 years old) female grizzly bears, and a sample of independent male bears, with a variety of radio-transmitters and duty cycle configurations, all of which had 6-hr mortality sensors, including: very high frequency (VHF) neck-mounted collars (Telonics, Inc., Mesa, AZ); VHF ear-tag transmitters (Advanced Telemetry Systems, Inc., Isanti, MN); standard GPS collars (TGW-4500, Telonics, Inc.); GPS-Argos collars (Models TGW-3580 and TGW-3583, Telonics, Inc.); and spread-spectrum collars (TGW-3690, Telonics, Inc.). All GPS transmitters were programmed to obtain a location once every 1–4 hrs. We programmed GPS units to turn off during the normal winter denning period to preserve battery life (Nov/Dec through Mar/Apr), and equipped GPS collars with automatic release mechanisms (CR2A; Telonics, Inc.), allowing the collars to release from the bear after 2 years or 3 years for subadults and adults, respectively.

Bears were captured under various circumstances, primarily: (1) at research capture sites distributed throughout the study area designed to capture a random sample of grizzly bears for monitoring vital rates; and (2) at or near bear-human conflict sites where specific bear(s) were targeted for conflict management (Mace et al. 2012). Additionally, a few bears were captured: (3) at capture sites for bears intended for translocation to augment the CYE population that did not meet the augmentation qualifications; and (4) at capture sites for other localized grizzly bear research; and (5) in traps set for other species (e.g., wolves or coyotes). All radio-marked bears were included in our analyses (except for bears translocated to the CYE), but each was assigned to one of two samples: research (i.e., random) or non-random (i.e., conflict-biased, Schwartz et al. 2006). The research sample included any bear captured at a NCDE research capture site and inclusion in this sample was retained throughout the full or remaining life of that transmitter. The non-random sample included any bear captured at other sites, but only if it was not already wearing a transmitter as part of the research sample. This included non-target captures of bears likely not involved in the specific conflict associated with the site. Thus, a bear in the non-random sample could transition to the research sample if it was captured at a research site, but a bear in the research sample captured at a conflict site retained its place in the research sample (Schwartz et al. 2006).

We captured research bears throughout the study area. Based on the DMA subunits, we distributed our sample of research females roughly in proportion to relative grizzly bear density, based on the distribution of female bears detected at DNA hair traps in 2004 (Kendall et al. 2009). We focused capture efforts in undeveloped areas, mostly on public lands, where estimated densities were highest.

The intensity of monitoring sometimes differed between the research and the non-random samples. Monthly monitoring and investigation of potential mortalities was prioritized for the research

sample. Localized monitoring for further conflict activity was the primary goal for many bears in the non-random sample, although these bears were included during research telemetry flights as possible. We often lost radio-contact with conflict bears, especially those individuals that had been translocated. Therefore, fate of these bears was not always ascertained with certainty. Using aerial and ground telemetry, or internet downloads of Argos data, monthly monitoring for research bears generally began in Mar/Apr and concluded in Nov/Dec as weather permitted, with only occasional flights occurring during the denning season. We attempted to investigate mortality signals from VHF monitoring or stationary locations persisting for $\geq$24 hrs from downloaded data within 2 weeks, to ascertain whether the bear had died. 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 MTFWP laboratory for further analyses.

Management Covariates

Bears involved in bear-human conflict might have different mortality and/or natality rates than bears not involved in conflict, especially in the years immediately following the conflict (Blanchard and Knight 1995, Haroldson et al. 2006). In addition, translocation can incur survival costs if bears are likely to encounter roads and other mortality sources in the new area or when homing to their previous range (Blanchard and Knight 1995, Comly-Gericke and Vaughan 1997). Recognizing that bears involved in conflicts are more likely to be captured and radio-marked than other bears, and that this might bias estimates of vital rates, Mace et al. (2012) restricted their analysis of vital rates in the NCDE to bears in the research sample with the understanding that some research-captured bears might be involved in conflict situations. Yet, in their efforts to respond to and mitigate bear-human conflict situations, state and tribal agency personnel monitor a sizable number of grizzly bears (~30) each year in the NCDE. In order to take advantage of the data provided by this monitoring, we developed a series of management-related individual covariates to quantify the potential effect of conflict on survival and other vital rates, and incorporated all monitoring data into our analyses (Haroldson et al. 2006).

We assigned a covariate for each bear-year representing whether or not the bear was involved in a management action during the current year (Mgmt1). This coding classified bears with no history of management action the same as bears whose last action occurred any time prior to the current year. We also developed a series of reverse-trend covariates to evaluate potential longer-term effects from 2 to 4 years as described by Haroldson et al. (2006). For example, to assess a 2-year management effect (Mgmt2), bears were coded as a 2 during the year(s) they were involved in management actions, 1 during the next year, and 0 during the next and any other year (assuming no further management action after the

first), and bears with no history of conflict were coded as a 0 for each year they were monitored. Thus, this coding classified bears with no history of management action the same as bears whose last management action was 2 years prior to the current year. Similar covariates were developed for 3-year (Mgmt3) and 4-year (Mgmt4) effects. We selected the best-fitting Mgmt covariate for each analysis using AIC_c and a preliminary set of global models with varying Mgmt covariates. To investigate the potential additive effect of management translocation, we also assigned an individual covariate for translocation distance (TrDist) corresponding to the most recent translocation (if any) for each individual. Translocation distances were truncated at 100 km and standardized by dividing by 100 km, thus resulting in a value ranging from 0 to 1. This covariate was entered only as an additive interaction term with Mgmt, thus constraining the distance value to decline with years since last management action. For example, for a bear translocated 50 km, values for Mgmt2 $\times$ TrDist equaled 1 (2×0.50) during the years of management action, 0.5 (1×0.50) for the year after, and 0 (0×0.50) for year(s) ≥ 2 years after the management action. Focusing on the research sample, we quantified the proportions of female and male bears in the population that were likely involved in bear-human conflict, and we estimated mean values for these management covariates. These mean covariate values were incorporated into estimates of independent bear survival (below), as well as estimates of cub and yearling survival (Section 4.6) and reproductive parameters (Section 4.7).

Independent Bear Survival

We estimated survival of independent bears during 2004–2013 using the known-fate routine within Program MARK (White and Burnham 1999) using the logit link. Data from 2014 was not included in the known-fate analysis, because fates of some independent bears monitored during 2014 could not be verified until the time of den emergence during 2015 (after analyses were initiated). Encounter histories were created for each bear-year with 12 encounter occasions corresponding with months. 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 (Haroldson et al. 2006). 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-transmitter (Haroldson et al. 2006).

Fates of some bears, particularly those among the male non-random sample, were not determined due to lost contact (unexplained) or failure to locate or investigate mortality signals (unresolved). Fate at

last telemetry contact was ascertained through later observations for some of these bears, and these discovered fates were utilized in analyses without a bias (Appendix A). For survival estimation, we ran two analyses (Haroldson et al. 2006). In the first analysis, bears with unexplained or unresolved fates were censored after the last month of monitoring, thus assuming no mortality. For the second analysis, these bears were assumed dead during the last month of monitoring. This approach yielded high and low survival rate estimates that likely bound true survival of the sampled population (Heisey and Fuller 1985, Pollock et al. 1989).

We modeled independent bear survival using 2 temporal (Season, Year) and 2 individual covariates (management history [Mgmt], and translocation distance [TrDist]) and an a priori set of 6 candidate models. The base model included Season (categorical variable: spring/summer = Apr–Jul, fall = Aug–Nov, winter = Dec–Mar). Other models included combinations of the continuous variables Mgmt, Mgmt × TrDist, and Year. Year was entered as a continuous variable, allowing us to evaluate a linear trend over time. Covariates were only assigned to months during the active season. Models were evaluated using Akaike's information criterion (AIC) adjusted for small sample sizes (i.e., AIC_c). Model-averaged survival estimates were calculated using mean covariate values for bears captured as part of the research sample.

We designed our survival analyses to obtain a single estimate for independent female and male bears irrespective of age, so that survival rates could be used to estimate thresholds for sustainable mortality among all independent bears (Section 4.11). In addition, preliminary modeling indicated that age-specific models performed no better than models with a single age class according to AIC_c. Similar results were obtained for the GYE, where age class explained little of the variation in survival rates of independent bears (Haroldson et al. 2006), and population projections incorporating age-specific survival among independent bears contributed little compared to those with a single estimate of survival (van Manen et al. 2014).

Spatial Distribution of Sample

We estimated the spatial distribution of our radio-marked sample based on those individuals monitored for independent bear survival, as this was the largest sample among all of our demographic analyses. Using GIS, we characterized all locations for these individuals during the years they were monitored to determine if locations were inside or outside of the DMA and to assign the DMA subunit when inside the DMA. For each bear-year, we summarized proportions by year and sex. We also determined the proportion of radio-marked deaths that occurred inside and outside of the DMA.

Results

Management History in the Research Sample

During 2004–2014, there were 323 captures of independent bears (170F, 153 M) at research trap sites. The research sample included 262 individuals (130F, 132M) captured 1–3 times. Among this sample, 4% were involved in management action(s) during the year of capture, and 19% were involved before or during the year of capture, with years since last management action ranging from 0 to 15 years (Figure 4.5.1). Similarly, 3% were translocated during the year of capture, and 14% were translocated before or during the year of capture. Translocation distance ranged from 0 to 215 km for bears involved in management actions. Including zeros for bears that were not involved in management actions or translocated, mean estimates of management covariates were slightly higher for males than for females (Table 4.5.1). These mean covariate values for the research sample were used to obtain population-wide estimates of independent bear survival. The proportion of research-sampled bears fitted with radio-transmitters reflected the focus on documenting female demographics: 98% of females and 44% of males.
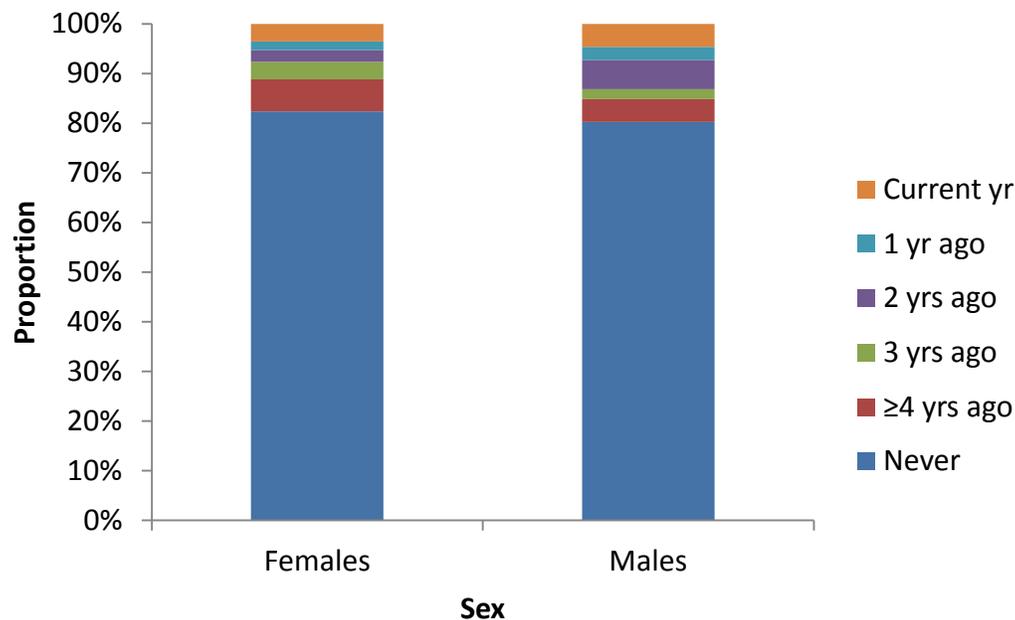
Figure 4.5.1. Proportions of independent (≥2 years old), research-captured female and male grizzly bears involved in management action(s), NCDE, 2004–2014.

Table 4.5.1. Mean values of management covariates for 322 independent (≥2 years old) female and male grizzly bears captured at research trap sites, NCDE, 2004–2014.

Covariate	Females	Males
Mgmt1	0.04	0.05
Mgmt2	0.09	0.12
Mgmt3	0.16	0.25
Mgmt4	0.28	0.40
TrDist[a]	0.20	0.52

[a] TrDist was estimated for bears with history of management only.

Female Survival

We estimated independent female survival for 169 individual bears monitored during 3,441 total months within 453 bear-years. Bears monitored as part of the research sample contributed about 76% of the data for this analysis (Table 4.5.2). Twenty-one mortalities were confirmed: 14 (67%) were human-caused, 3 (14%) were likely natural-caused, and 4 (19%) were of undetermined cause. No mortalities occurred in winter dens. Human-caused mortalities included management removals (6), defense of life kills (2), poaching/malicious kills (2), illegal defense of property kills (2), and collisions with a vehicle (1) and a train (1). Predation by another bear was the cause of 1 natural mortality; causes for the other 2 were undetermined, but circumstances suggested humans were not involved. Fates of 6 other bears were unexplained (5) or unresolved (1).

In preliminary modeling, the global model with Mgmt2 ranked highest compared to global models with the other reverse-trend management covariates, indicating the survival effect of management action extended over 2 years. This result was the same using either data set (i.e., unknown fates censored or assumed dead). In our model set, AIC_c ranking was also the same using the two sets of data. "Season + Mgmt2" was the top model, and the covariate Mgmt2 was present in all of the 3 top models (Table 4.5.3). Compared to the base model, inclusion of Mgmt2 improved AIC_c by 5.8 units using the censored data set and by 11.2 units using the assumed-dead data set. Independent of Mgmt2, addition of the covariates TrDist and Year did not improve AIC_c from the base model.

Using mean covariate values for the research sample (Table 4.5.1), monthly estimates of survival were highest during the denning season and lowest during fall. Annual survival estimates were relatively similar comparing the analysis with the censored unknown fates (0.951) versus the assumed dead censored fates (0.943; Table 4.5.4). Mgmt2 was the only covariate with 95% CIs that did not bound zero, and its effect size was large. The 2-year management effect indicated involvement in management actions negatively affected survival during the management year and the years following (Figure 4.5.2). Using model averaging and holding TrDist constant at 0 and year constant at the mean, estimated annual

Table 4.5.2. Samples available for analysis of independent (≥2 years old) female and male survival of grizzly bears, NCDE, 2004–2013.

		Encounter histories analyzed		
Sex	Sample	No. individuals[a]	No. bear-years[a,b]	No. months
Female	Research	117	326	2,600
	Non-random	57	127	841
	Total	164	453	3,441
Male	Research	47	73	340
	Non-random	85	137	570
	Total	124	209	910

[a] Column may not sum because individuals can transition between samples and age classes.
[b] Includes partial years (i.e., <12 months of monitoring).

Table 4.5.3. AIC_c model selection information for known-fate survival models of independent (≥2 years old) female survival of grizzly bears, NCDE, 2004–2013.

Data set	Model	AIC_c	ΔAIC_c	Weight	k
Censored	Season + Mgmt2	234.60	0	0.43	3
	Season + Mgmt2 + Mgmt2 × TrDist	235.99	1.39	0.21	4
	Season + Mgmt2 + Year	236.01	1.41	0.21	4
	Season + Mgmt2 + Mgmt2 × TrDist + Year	237.28	2.68	0.11	5
	Season	240.36	5.76	0.02	2
	Season + Year	241.78	7.18	0.01	3
Assumed Dead	Season + Mgmt2	282.03	0	0.49	3
	Season + Mgmt2 + Mgmt2 × TrDist	283.67	1.65	0.22	4
	Season + Mgmt2 + Year	283.84	1.82	0.20	4
	Season + Mgmt2 + Mgmt2 × TrDist + Year	285.43	3.41	0.09	5
	Season	293.22	11.19	0.00	2
	Season + Year	295.03	13.01	0.00	3

survival was 0.11–0.17 lower for bears involved in management actions during the current year compared to bears involved in actions ≥2 years ago or bears with no management history, although 95% CIs overlapped among estimates. The beta coefficient for TrDist was negative, however its 95% CIs overlapped zero and the effect size was smaller. Holding Mgmt2 constant at 2 and year constant at the mean, estimated annual survival was 0.04–0.06 lower for bears translocated ≥100 km compared to those not translocated. Again, 95% CIs overlapped for these estimates. There was no discernible change in annual survival over the 2004-2013 study period.

Table 4.5.4. Estimates of independent (≥2 years old) grizzly bear survival, NCDE, 2004–2013.

Sex	Treatment of unknown fates	Estimate	SE	Lower 95% CI	Upper 95% CI
Female	Censored	0.951	0.013	0.917	0.972
	Assumed dead	0.943	0.014	0.907	0.965
Male	Censored	0.916	0.044	0.782	0.971
	Assumed dead	0.805	0.065	0.648	0.903

Male Survival

We estimated male survival for 124 individual bears monitored during 910 total months within 209 bear-years. Bears monitored as part of the research sample contributed about 37% of the data for this analysis (Table 4.5.2). Twenty-four mortalities were confirmed: 21 (88%) were human-caused and 3 (12%) were of undetermined cause. No mortalities occurred in winter dens. Human-caused mortalities included management removals (10), poaching/malicious kills (3), illegal defense of property kills (2), defense of life kills (2), and collisions with vehicles (2) and trains (2). Fates of 9 other bears were unexplained (7) or unresolved (2).

In preliminary modeling, the global model with Mgmt4 ranked highest compared to the global models with the other reverse-trend covariates, indicating the survival effect of management action extended over 4 years. This result was the same using either the censored or assumed-dead data set. In our model set, AIC_c ranking was the same using the two sets of data. Mgmt4 was present in all 3 of the top models (Table 4.5.5). Compared to the base model, inclusion of Mgmt4 improved AIC_c by 10.4 units using the censored data set and by 5.4 units using the assumed-dead data set. Independent of Mgmt4, addition of the covariates TrDist and Year did not improve AIC_c from the base model.

Using mean covariate values for the research sample (Table 4.5.1), monthly estimates of survival were highest during the denning season and roughly equal during spring/summer and fall using either data set. Annual survival estimates varied widely comparing the analysis with the censored unknown fates (0.916) versus the assumed dead censored fates (0.805; Table 4.5.4). Mgmt4 was the only covariate with 95% CIs that did not bound zero, and its effect size was large. Holding other covariates constant, annual survival was 0.25–0.33 lower for bears involved in management actions during the current year compared to bears involved in actions ≥4 years ago and bears with no management history (Figure 4.5.2). We detected no additive effect of translocation distance or year on annual survival rates.
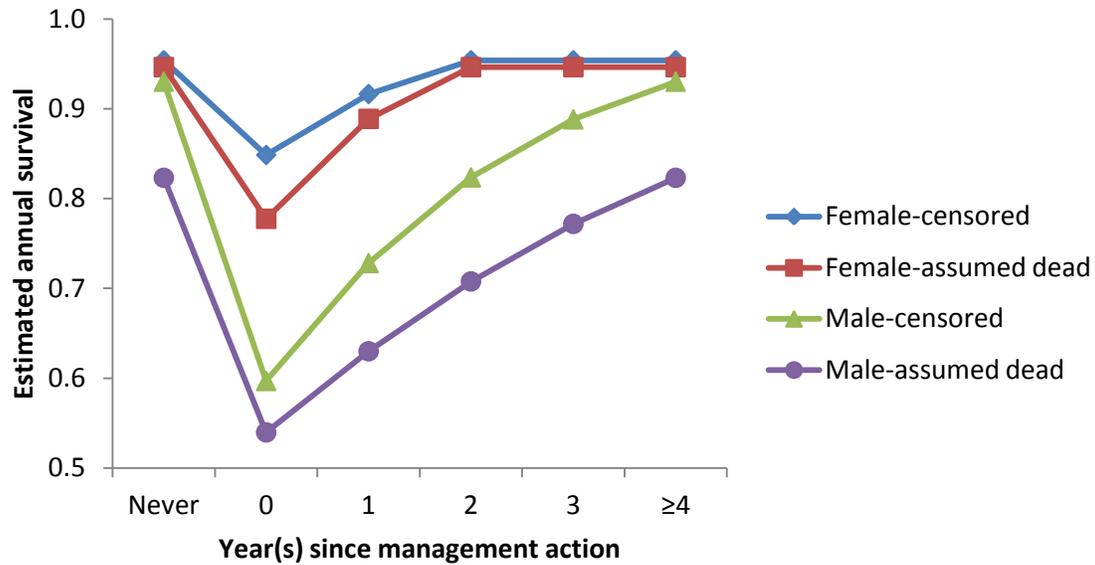
Figure 4.5.2. Estimated annual survival of independent (≥2 years old) female and male grizzly bears as influenced by involvement in management actions, NCDE, 2004–2013. Estimates shown were obtained using data sets where bears with unknown fates were censored after their last location or assumed dead at their last location. Reverse-trend modelling indicated best fit for a 2-year management effect for female survival and a 4-year management effect for male survival. Management covariates were present in all of the top models and improved AIC$_c$ by ≥5.4 units. Estimates were based on model averaging, where values were held constant at 0 for translocation distance and at the mean for year.

Table 4.5.5. AIC$_c$ model selection information for known-fate survival models of independent (≥2 years old) male survival of grizzly bears, NCDE, 2004–2013.

Data set	Model	AIC$_c$	ΔAIC$_c$	Weight	k
Censored	Season + Mgmt4	202.89	0	0.44	3
	Season + Mgmt4 + Year	203.72	0.82	0.29	4
	Season + Mgmt4 + Mgmt4 × TrDist	204.89	1.99	0.16	4
	Season + Mgmt4 + Mgmt4 × TrDist + Year	205.71	2.82	0.11	5
	Season	213.25	10.35	0.00	2
	Season + Year	214.17	11.27	0.00	3
Assumed Dead	Season + Mgmt4	264.19	0	0.42	3
	Season + Mgmt4 + Year	265.31	1.12	0.24	4
	Season + Mgmt4 + Mgmt4 × TrDist	265.85	1.66	0.18	4
	Season + Mgmt4 + Mgmt4 × TrDist + Year	266.98	2.79	0.10	5
	Season	269.54	5.35	0.03	2
	Season + Year	270.73	6.54	0.02	3

Spatial Distribution of Sample

The spatial distribution of locations indicated our sample was representative of the population residing within the DMA. In our sample of bears monitored for independent survival during 2004–2013, 85% of females (*n* = 164) and 79% of males (*n* = 124) had locations entirely within the DMA. Approximately 92% of female bear locations and 95% of male locations occurred within the DMA, when standardized by bear-year (Table 4.5.6). Bears that spent significant time outside of the DMA (>50% of locations) were either bears that crossed the US-Canada border north of the DMA (*n* = 6) or bears that utilized the Blackfeet Reservation and/or the East Front subunits on the eastern border of the DMA (*n* = 5). Ninety-six percent of radio-marked bear deaths (*n* = 47) occurred inside the DMA. The two deaths that occurred outside the DMA were males and both occurred outside the eastern border of the DMA.

Based on bear locations, we estimated the minimum number of radio-marked bears that used each of the DMA subunits within each year. We documented use of all 9 DMA subunits by radio-marked females during all years but 2004, when females used 8 of 9 subunits. We documented use of all 9 subunits by radio-marked males during 4 years, use of 8 subunits during 3 years, use of 7 subunits during 2 years, and use of 6 subunits during 1 year. Generally, as intended, subunits with higher relative densities (Section 4.3) also had higher representation in our radio-marked sample (Table 4.5.6). However, Glacier National Park and the Middle Fork of the Flathead River subunits appeared underrepresented in our monitored sample based on relative density estimates. This discrepancy was largely attributable to restrictions and/or impediments to trapping in Glacier National Park and the large wilderness areas situated in the interior of the DMA.

Table 4.5.6. Minimum number of radio-marked, independent (≥2 years old) grizzly bears[a] using the 9 DMA subunits or areas outside the DMA, with estimated proportion of locations within each, NCDE, 2004–2013. For each sex, DMA subunits are ordered by descending use and relative densities of grizzly bears in 2004 are shown for comparison (based on Kendall et al. 2009; see Section 4.3).

| Sex | DMA subunit | Minimum individuals/yr | | Proportion of locations[b] | Relative density[c] |
		Mean	Range		
Female	South Fork Flathead River-Swan Valley	13.2	7 − 18	0.23	0.13
	Glacier National Park	12.3	6 − 18	0.16	0.44
	East Front	9.5	3 − 16	0.15	0.09
	North Fork Flathead River	8.6	5 − 12	0.13	0.18
	Blackfeet Reservation	6.9	4 − 11	0.08	0.13
	Middle Fork Flathead River	4.9	1 − 9	0.04	0.20
	South End	4.7	0 − 7	0.07	0.07
	Flathead Reservation	3.5	1 − 6	0.04	0.05
	Salish-Island	1.8	1 − 4	0.01	0.06
	Outside DMA	6.6	4 − 12	0.08	
Male	South Fork Flathead River-Swan Valley	7.6	3 − 12	0.30	0.28
	East Front	5.4	1 − 12	0.21	0.17
	North Fork Flathead River	3.9	1 − 8	0.10	0.48
	Glacier National Park	3.3	0 − 8	0.09	0.82
	Blackfeet Reservation	2.8	0 − 4	0.08	0.25
	Middle Fork Flathead River	2.4	0 − 7	0.05	0.55
	South End	2.4	0 − 6	0.06	0.08
	Flathead Reservation	1.5	0 − 4	0.03	0.04
	Salish-Island	1.1	0 − 3	0.02	0.11
	Outside DMA	2.9	1 − 6	0.05	

[a] The sample of bears used for estimation of independent survival, including bears in the research and non-random sample.
[b] Estimates standardized by bear-year.
[c] Cells with >0 summed probability (Table 4.3.2).

4.6 Demographic Monitoring: Cub and Yearling Survival

Along with independent bear survival, estimates of juvenile survival rates are necessary for evaluating population growth and trajectory. In grizzly bears, survival of dependent young is typically lower than that of adults or subadults (Schwartz et al. 2003). Grizzly bear offspring are small at birth and exhibit tremendous growth during their first two years. Consequently, radio-collaring of cubs and yearling is uncommon, and juvenile survival is most often estimated by documenting the presence or absence of offspring accompanying radio-marked females over time. Using this approach, we estimated annual survival rates of cub and yearling grizzly bears in the NCDE and tested for a temporal trend and management effects.

Methods

We conducted observation flights in early spring to ascertain the reproductive status of each adult female, including age class of offspring (i.e., cubs, yearlings, or 2-year-olds) and litter size. Whenever possible, we continued visually monitoring reproductive status during telemetry flights to document offspring survival from changes in litter size. We estimated cub and yearling survival using the nest success routine (Dinsmore et al. 2002) in Program MARK, following methods detailed in Schwartz et al. (2006) and Mace et al. (2012). This technique is suited for intermittent observations of mothers with dependent offspring and assumes mortality has occurred within a given interval if an offspring observed at the previous observation is absent at the current observation of its mother. Litters enter and exit the analysis dependent on their first and last observation dates, and a daily survival probability is calculated using only those individuals under observation on a given day. Using sequential observations of radio-marked females with cubs and/or yearling litters, we estimated daily survival throughout the cub and yearling active seasons, spanning the days between the first observation(s) of cubs in the spring of the cub year and the last observation(s) of yearling in the fall of the yearling year. Numbering the days throughout this interval (579 days), we developed encounter histories for each offspring which included: (1) the first day the offspring was observed with its mother; (2) the last day the offspring was known to be present with its mother; (3) the last day the mother was monitored; and (4) a code for alive or presumed dead. For offspring that survived, (2) and (3) were equal. If mortality occurred, the last day the mother was monitored was equal to the first day she was observed without the offspring in question. Thus, days (2) and (3) could differ for offspring within the same litter if partial litter loss was observed. We estimated survival of dependent offspring for 3 time periods. The cub active period began the day of our first observation of a cub litter following den emergence (day 1 = 17 April) and ended on the day of our elast cub observation prior to den entry (day 235 = 7 Dec). The winter denning period began on day 236

and ended on day 356. The yearling active period began the day of our first observation of a yearling litter following den emergence (day 357 = 8 April) and ended the day of our last yearling observation prior to den entry (day 579 = 16 Nov). We determined survival for each period by raising the daily survival rate to the power corresponding to the number of days in the period: 235 for the cub period, 121 for the denning period, and 223 for the yearling period.

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). To quantify overdispersion (i.e., $\hat{c}$), we followed the methods of Bishop et al. (2008). We used the bootstrap procedure in Program MARK 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 cub and yearling survival estimates.

We modeled cub and yearling survival using 2 temporal (Period, Year) and 2 individual covariates associated with the mother (Mgmt, TrDist [Section 4.1]) and an a priori set of 6 candidate models. The base model included Period (categorical variable: cub active, denning, yearling active) only. Other models included combinations of the continuous variables Mgmt, Mgmt × TrDist, and Year. Year was entered as a continuous variable, allowing us to evaluate a linear trend over time. Covariates were only assigned to months during the active season. Models were evaluated using AIC adjusted for small sample sizes and overdispersion (i.e., QAIC$_c$). Model-averaged survival estimates were calculated using mean covariate values for bears captured as part of the research sample (Table 4.5.1).

Results

We estimated cub and/or yearling survival of 176 offspring in 89 litters during a total of 39,070 bear-days. We obtained the sample by monitoring 1–3 distinct litters of 72 different mothers. Offspring monitored as part of the research sample contributed about 68% of the data for this analysis (Table 4.6.1).

We documented 65 known or probable mortalities. Based on the interval between the last date observed and the first date missing, 39 mortalities occurred during the cub active period, 20 occurred during the yearling active period, and the timing of 6 could not be definitively assigned to either period. Known or probable causes of death were natural (68%), management removals (11%), mortality associated with self-defense kills of mothers (6%), vehicle collisions (5%), mortality following

translocation of family group (5%), mortality associated with illegal kill of mother (3%), and mortality associated with death of mother from an unknown cause (3%).

Our calculated estimate of overdispersion, $\hat{c}$, was 1.56, indicating a moderate degree of within-litter correlation in survival. This value was used to inflate the variance in our estimates to account for the lack independence. A lack of complete independence was also evident when we examined the relative frequency of partial versus whole litter loss (Table 4.6.2). Among multi-cub litters with ≥ 1 mortality, 60–65% of these litters experienced whole litter loss, and a number of times it was due to the mortality of the mother. Incremental whole litter loss was observed within 2 litters.

Table 4.6.1. Samples available for analysis of cub and yearling grizzly bear survival, NCDE, 2004–2013.

| Sample | Period | Encounter histories analyzed | | |
		No. individuals[a]	No. litters[a]	No. days
Research	Cub (active)	101	52	12,214
	Den	52	30	6,292
	Yearling (active)	69	38	7,935
	Total	118	60	26,441
Non-random	Cub (active)	45	22	5,151
	Den	27	13	3,267
	Yearling (active)	40	20	4,211
	Total	58	29	12,629
Total		176	89	39,070

[a] Column may not sum because not all individuals were monitored during all periods.

Table 4.6.2. Percentage of partial versus whole litter loss among cub and yearling grizzly bear litters that experienced ≥1 mortality, NCDE, 2004–2013.

| Litter size | n | Litter loss | | Whole loss because mother died |
		Partial	Whole	
1	7		1.00	0.14
2	26	0.35	0.65	0.23
3	5	0.40	0.60	0.20
Total	38	0.29	0.71	0.18

Mgmt1 ranked highest among the management covariates in preliminary modeling, therefore it was used in model selection for the full model set. The base model (Period only) ranked highest according to QAIC$_c$, with 46% of the QAIC$_c$ weight (Table 4.6.3). Based on mean values of covariates for research females (Table 4.5.1), model-averaged annual survival estimates were 0.55 for cubs and 0.64 for yearlings (Table 4.6.4). Beta coefficients for all covariates in all models had 95% CIs that overlapped zero, and effect sizes were small for most (i.e., predicted change in survival over the range of covariate values was similar to overall variation in survival). The one covariate with a large effect size was translocation distance, but only for the cub period. Estimating for years of management action and mean year, model-predicted cub survival declined from 0.45 when translocation distance was 0 to 0.16 when translocation distance was ≥100 km. Nevertheless, the 95% CIs were very large for both estimates, therefore they overlapped extensively.

Table 4.6.3. QAIC$_c$ model selection information for daily-survival models of cub and yearling grizzly bear survival, NCDE, 2004–2013.

Model	QAICc	ΔQAICc	Weight	k
Period	342.384	0.000	0.39	2
Period + Mgmt1	342.937	0.553	0.30	4
Period + Mgmt1 + Mgmt1 × TrDist	344.046	1.662	0.17	6
Period + Year	346.111	3.727	0.06	4
Period + Mgmt1 + Year	346.610	4.226	0.05	6
Period + Mgmt1 + Mgmt1 × TrDist + Year	347.326	4.942	0.03	8

Table 4.6.4. Estimates of daily and annual, cub and yearling grizzly bear survival, NCDE, 2004–2013.

	Daily				Annual			
	Estimate	SE	Lower 95% CI	Upper 95% CI	Estimate	SE	Lower 95% CI	Upper 95% CI
Cub	0.997	0.0005	0.996	0.999	0.553	0.070	0.432	0.708
Yearling	0.998	0.0006	0.997	0.999	0.639	0.080	0.502	0.816

4.7 Demographic Monitoring: Reproductive Output

Along with survival rates, the reproductive output of a population is central to understanding its potential for growth. Grizzly bear offspring typically stay with their mother until they are two years old, therefore a successful reproductive cycle spans 3 years for female grizzly bears. Quantifying the reproductive output of a grizzly bear population, thus, requires an understanding of the relative numbers of females with cub, yearling, and two-year-old offspring; litter sizes produced; and the range of ages when females first produce a litter. In this section, we examined these characteristics of grizzly bear reproduction in the NCDE, tested for management effects, and evaluated temporal trends in rates.

Methods

Transition probabilities

Based on sequential annual observations of reproductive status for females ≥3 years old, and using the multi-state model in Program MARK, we estimated the probabilities of transitioning from a given reproductive state in one year to another reproductive state in the following year (Schwartz and White 2008). Females begin each year in one of the following states: no young (N), with dependent cubs (C), with dependent yearlings (Y), or with dependent 2-year-olds (T). There are 10 biologically feasible year-to-year transitions between these states: NN, NC, CN, CC, CY, YN, YC, YT, TN, and TC. We modeled transition probabilities with 1 temporal (Year) and 2 individual covariates (Mgmt1, TrDist [Section 4.1]) and an a priori set of 6 models. Year was entered as a continuous variable, allowing us to evaluate a linear trend over time. These covariates were applied only to the NC transition, because: (1) our primary interest in this analysis was estimation of the proportion of females with cubs and this transition should be most sensitive to potential effects of covariates; and (2) effects of covariates on dependent offspring survival (involved in most other transitions) were more thoroughly tested in analyses of cub and yearling survival (Section 4.6). Model-averaged transition probabilities were calculated using mean covariate values for bears captured as part of the research sample (Table 4.5.1). We calculated stable state probabilities and confidence intervals for each reproductive state by bootstrapping (Efron and Gong 1983) as described by Schwartz and White (2008).

Litter Size

We attempted to obtain visual observations of radio-marked adult females as close to den emergence as possible to determine reproductive status and litter size, however dates of first observations varied. Therefore, some cub mortality likely occurred after den emergence and prior to our first

observation, which would bias our estimates of litter size low (Schwartz et al. 2006). To account for this, we used observed litter sizes, their date of first observation, and our estimated daily cub survival rate to adjust mean litter size, similar to the approach of Schwartz et al. (2006). For each litter, we calculated the number of days between its first observation and the earliest observation of any cub litter (i.e., den emergence [17 April]). The product of the number of post emergence days and the daily cub survival rate is an estimate of the probability that a cub survived to the observation date ($P_{live\ cub}$). Therefore, $1 - P_{live\ cub}$ is an estimate of the probability that a cub did not survive to the observation date ($P_{dead\ cub}$). For each litter observed after 17 April, probabilities that the litter consisted of 1, 2, or 3 cubs at den emergence were derived using the equations in Table 4.7.1. A maximum litter size of 3 cubs was assumed, therefore the estimated probabilities of 1-, 2-, and 3-cub litters summed to 1 for each observed litter size. These equations also assumed independence among litter mates. Mean adjusted litter size was calculated from the mean probabilities of 1-, 2-, and 3-cub litters.

Age of Primiparity and Reproductive Longevity

We obtained an unbiased estimate of mean age of primiparity using the method of Garshelis et al. (1998), which utilizes information from all females observed starting at the earliest observed age of litter production and censors females lost from monitoring due to transmitter loss or mortality. We estimated confidence intervals for the age of primaparity using bootstrapping techniques in the PopTools 3.1.1. add-in for Excel 2007. We documented the oldest age of litter production based on observations of reproductive status of monitored females.

Table 4.7.1. Formulas for estimating the probabilities that a litter observed after den emergence consisted of 1, 2, or 3 cubs at den emergence. A maximum litter size of 3 cubs was assumed, therefore the estimated probabilities of 1-, 2-, and 3-cub litters summed to 1 for each observed litter size. Litter size probabilities were derived based on the probability that a non-surviving cub previously existed ($P_{dead\ cub}$), which was $1 - $ (numbers of post emergence days [before the litter observation] × estimated daily cub survival rate).

Observed litter size	Estimated probability of litter size (at den emergence)		
	1 cub	2 cubs	3 cubs
1 cub	$1 - P_{dead\ cub} - P_{dead\ cub}^2$	$P_{dead\ cub}$	$P_{dead\ cub}^2$
2 cubs	0	$1 - P_{dead\ cub}$	$P_{dead\ cub}$
3 cubs	0	0	1

Results

Transition Probabilities

We documented 232 reproductive transitions for 114 females. Number of transitions per female ranged from 1 to 9, with mean of 2.0. Females monitored as part of the research sample contributed 77% of the data for this analysis (Table 4.7.2).

In preliminary models with covariates applied to the NC transition, Mgmt2 ranked highest among management covariates, therefore it was used in model selection. Year was present in the two top models, but inclusion of this covariate only improved AIC_c by 1.39 over the base model (Table 4.7.3). Addition of Mgmt2 and TrDist did not improve AIC_c. Year was the only covariate with 95% CIs that did not bound zero.

Using mean covariate values for the research sample (Table 4.5.1), the steady state asymptotic estimate of the proportion of females with cubs was 0.287 (Table 4.7.4). The year effect indicated a slight increase in this proportion over the study period, from 0.266 to 0.304, however 95% CIs for these estimates overlapped extensively.

Table 4.7.2. Samples available for analysis of reproductive transition probabilities for female grizzly bears ≥3 years old, NCDE, 2004–2014.

Sample	Status at start of transition	Encounter histories analyzed	
		No. individuals	No. transitions
Research	None	65	101
	Cub	41	47
	Yearling	23	24
	2-year-old	7	7
	Total	90	179
Non-random	None	16	24
	Cub	13	15
	Yearling	9	10
	2-year-old	4	4
	Total	28	53
Total		114	232

Table 4.7.3. AIC$_c$ model selection information for multi-state models of female grizzly bear (≥3 years old) reproductive transition probabilities, NCDE, 2004–2014.

Model	AICc	ΔAICc	Weight	k
Base + Year	334.118	0.000	0.31	7
Base + Mgmt2 + Year	334.481	0.362	0.26	8
Base	335.511	1.392	0.16	6
Base + Mgmt2	335.823	1.705	0.13	7
Base + Mgmt2 + Mgmt2 × TrDist + Year	336.535	2.416	0.09	9
Base + Mgmt2 + Mgmt2 × TrDist	337.821	3.702	0.05	8

Table 4.7.4. Steady state proportions of reproductive states among adult (≥4 years old) female grizzly bears, NCDE, 2004–2014.

Reproductive state	Estimate of proportion	SE	Lower 95% CI	Upper 95% CI
None	0.339	0.073	0.195	0.483
With cubs	0.287	0.031	0.227	0.347
With yearlings	0.236	0.026	0.185	0.286
With 2-year-olds	0.139	0.041	0.058	0.220

Litter Size

We obtained 110 visual observations of cub litters for 90 individual females. Number of litters observed per female ranged from 1 to 3 with a mean of 1.2. First date of observation ranged from 17 April to 9 November, with a mean of 29 June. Females monitored as part of the research sample contributed 72% of the data for this analysis. Observed litter sizes ranged from 1 to 3, with a mean of 1.95. Estimated mean probabilities of 1-, 2-, and 3-cub litters at den emergence were 0.156, 0.590, and 0.254, equal to a mean adjusted litter size of 2.10.

Age of Primiparity and Reproductive Longevity

We observed no cub production for grizzly bears ≤3 years old, but documented reproductive status of 32 nulliparous females monitored for 1–4 years beginning at age 4. Females monitored as part of the research sample contributed 75% of the data for this analysis. We documented 18 first litters and censored 14 bears prior to first reproduction due to transmitter loss or mortality (Table 4.7.5). One nulliparous 7-year-old female was lost to radio-contact before we observed litter production, therefore we

assumed litter production at 8 years old to complete the calculation. Proportion of females having produced their first litter displayed a gradual increase between the ages of 4 and 8 (Figure 4.7.1). Our unbiased estimate of mean age of primaparity was 5.8 (95% CI = 5.3–6.3). The oldest female observed with a cub litter had an estimated age of 26 years and she carried this litter to at least age 27.

Table 4.7.5.   Calculation of unbiased mean age of primiparity for female grizzly bears, based on observations of reproductive status for previously nulliparous individuals, by age, NCDE, 2004–2014.

Age	n	Proportion of sample observed to produce first litter	Proportion in population available to produce first litter	Proportion in population producing first litter	Age × proportion of population producing first litter
4	31	0.19	100	0.19	0.77
5	17	0.35	0.81	0.28	1.42
6	8	0.38	0.52	0.20	1.17
7	4	0.75	0.33	0.24	1.71
8	1	1.00	0.08	0.08	0.65
					5.74
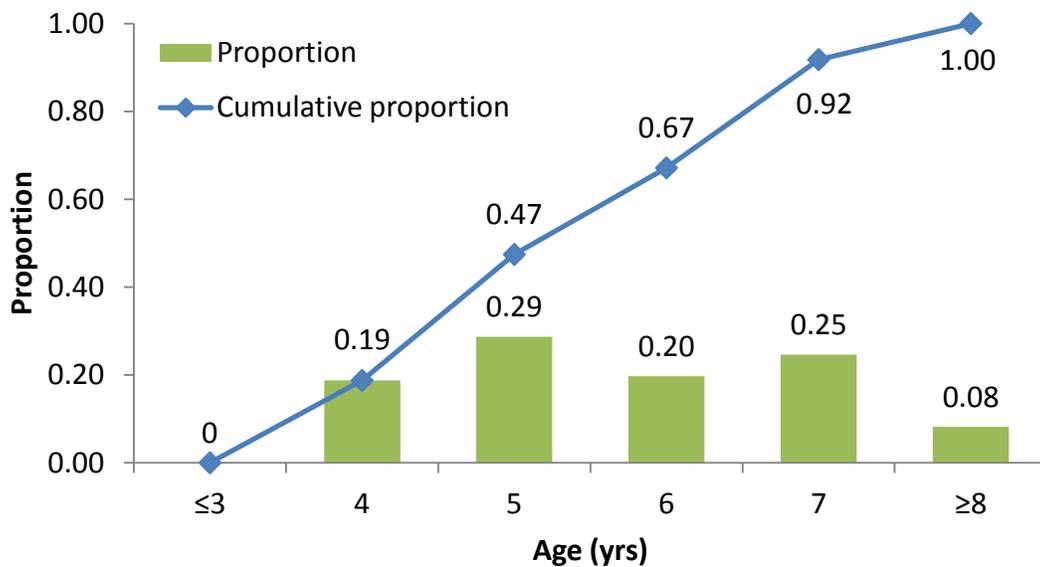
Figure 4.7.1. Proportion of female grizzly bears having produced their first litter, by age, NCDE, 2004–2014.
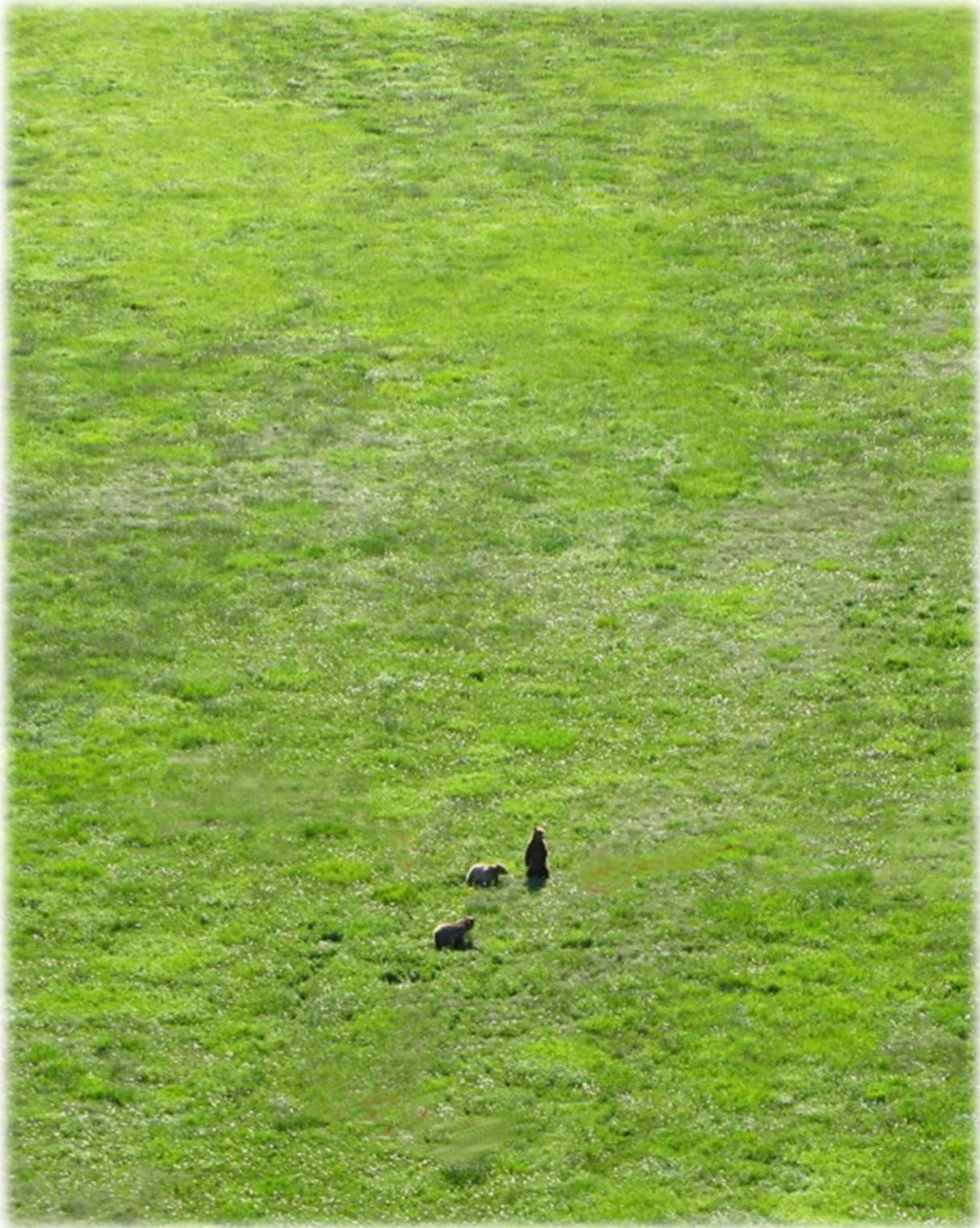
4.8 Population Age Structure

The ultimate goal of this monitoring program is to estimate the trend of the NCDE grizzly bear population using population modeling of our observed survival and reproductive rates. Along with an estimate of population growth rate, population modeling will also provide estimates of population sex-age structure. Alternatively, estimates of population sex-age structure can be derived from capture data and population reconstruction (Eberhardt and Knights 1996). Presumably, corroboration among these independent estimates of sex-age structure would lend credibility to our estimates of vital rates and population trend. Therefore, our goals for this section were: (1) to estimate the age structure of the NCDE grizzly bear population during 2004–2014 based on field data; (2) to compare the observed age structure to model-predicted stable age distribution based on observed vital rates; and (3) to use information from population structure to determine the most realistic estimate of independent male survival to use for further population modeling.

Methods

We estimated the age structure of the NCDE grizzly bear population using field data. Female and male structures were estimated separately, due to the potential sex bias in capture probability (Mace et al. 1994). Additionally, we only estimated the age structure for independent bears, due to the bias associated with lower capture probability and lower survival of the cub and yearling age classes (Mace et al. 1994). We estimated population age structure using two methods. First, using the research-capture sample for 2004-2014 (Section 4.4), we summed number of captures by age-at-capture (cementum age or estimated age [Section 4.5]) across all years for each sex. Individuals were only counted once per year, even if captured more than once/per year. Second, we used population reconstruction (Eberhardt and Knight 1996) to estimate the age structure for the total number of independent individuals known alive each year. This reconstruction sample included all bears captured for research and other reasons (i.e., research and non-random sample combined) during 1988–2014. Physical capture was necessary to estimate ages of bears, therefore the reconstruction sample was restricted to those bears that were captured on ≥1 occasion and for which known or estimated ages were obtained. For these captured bears, DNA detections were used as available to expand the range of years individual bears were known to be alive (USGS, unpublished data). To reconstruct the population, we back-dated each individual from age-at-capture to the year of birth and forward-dated to the last year it was known alive (by means of recapture, radio-telemetry, DNA detection, or documented mortality). Earliest birth years among our entire reconstructed sample dated back to 1961, however we estimated current age structure by summing number of bears by age for each sex only across the years 2004–2010. We truncated data at 2010 due to the potential

sampling bias among cohorts in recent years, which are underrepresented due to lower capture probability of dependent and young bears (Mace et al. 1994); and by our inability to include bears that might be captured in the future and back-dated to the present. The year 2010 was selected because the number of bears in the reconstructed sample steadily increased until that year and then abruptly declined. Using population reconstruction data from 1990–2010, we estimated mean and median age of independent bears, by sex, on an annual basis to examine changes over time.

Using estimated vital rates (Sections 4.5 to 4.7), we calculated the stable-age distribution for the NCDE population, using the software program RISKMAN 1.9.003 (www.riskman.nrdpfc.ca). RISKMAN is a computer simulation system, utilizing individually-based, stochastic population modeling, which is intended for risk assessment and decision-making. It employs Monte Carlo simulations to estimate the uncertainty of population trajectories, based on the uncertainty inherent in input demographic parameters and population size (Taylor et al. 2006). For each of our models (described below), we ran 2000 10-year simulations (i.e., runs), corresponding to the period 2005–2014. We used 28 age classes corresponding to the oldest observed age; set the minimum age of reproduction at 4 years; set the maximum age of reproduction at 28 years; and employed the annual model because all of our vital rates were annual estimates. Input parameters were as shown in Table 4.8.1, except as described below. As reported in section 4.5, our two estimates of independent female survival were relatively close (0.951 versus 0.943), therefore the mean value (0.947) was used in RISKMAN modeling. In contrast, the difference between our two estimates of independent male survival was quite large (0.916 versus 0.815), therefore we ran a series of RISKMAN models with varying levels of independent male survival ranging from 0.91 to 0.81. By comparing characteristics of the observed age structures to those of the model-predicted stable-age distributions (e.g., mean age, sex ratio), we evaluated which male survival rate, within our estimated range, was most consistent with the field data on bear age structure. To allow for a more direct comparison of the field data with model output, we fit a linear model to the observed age structures (research-captures and population reconstruction) using number of bears as the response and log-transformed age as the predictor. For our evaluation of fit between the two distributions, we used the standard deviation (SD) of the mean difference between age-specific proportions estimated from simulations versus observed age-at-capture data, whereby values closer to 0 indicated better fit. We also compared the model-predicted population sex ratio to that obtained from the ecosystem-wide DNA mark-recapture study conducted in 2004 (Kendall et al. 2009).

Results

Analysis of age structure from age-at-capture data for the research sample involved 315 (169 F, 146 M) captures of 254 (129 F, 125 M) independent bears during 2004–2014. Analysis of age structure

from population reconstruction involved 407 (195 F, 212 M) bears captured during 2004–2010 and known to be alive and ≥2 years old during a total of 1,716 (836 F, 880 M) bear-years.

Using field data, estimated age structures were nearly identical based on the research-captured sample and the sample obtained by population reconstruction, for both females (Figure 4.8.1) and males (Figure 4.8.2). The age distribution for females was flatter than that of males, with higher proportions of bears observed at older age classes. Mean and median ages of females were consistently higher than that of males, by approximately 1.5 to 2.0 years for most estimates (Table 4.8.2).

Using the population reconstruction data, mean ages of independent females and males showed an increasing trend during 1990–2010 (Figure 4.8.3). Median ages, less influenced by the extreme values of older bears, were relatively stable for males during the period. Median age of females increased during the 1990s and stabilized during the 2000s.

For females, there was relatively good fit comparing the field-derived age structure to the stable-age distribution obtained from RISKMAN modeling, especially among intermediate age classes (Figure 4.8.4). The SD for the mean difference between age-specific proportions was 0.008 when compared to the fitted research-capture age structure and 0.008 when compared to the fitted reconstruction age structure.

Table 4.8.1. Input parameter estimates used for stochastic modeling of NCDE grizzly bear populations with RISKMAN software.

Input parameter	Estimate	SE	Notes
Probability with 1 offspring	0.160		Held constant among models
Probability with 2 offspring	0.590		Held constant among models
Probability with 3 offspring	0.250		Held constant among models
Mean litter size	2.100	0.050	Held constant among models
Proportion with litters	0.287	0.031	Held constant among models
Male survival age 0	0.553	0.070	Held constant among models
Male survival age 1	0.639	0.080	Held constant among models
Male survival ages 2–28	0.895	0.054	Base rate, but varied for investigations
Female survival age 0	0.553	0.070	Held constant among models
Female survival age 1	0.639	0.080	Held constant among models
Female survival ages 2–28	0.947	0.014	Base rate, but varied for investigations
Initial population size	765	29.27	Base rate, but varied for investigations

For males, the fit of model-predicted stable-age distribution obtained from RISKMAN modeling to the field-derived age structures was best when independent male survival rate was approximately 0.89. Within the range of male survival rates, the SD for the mean difference between age-specific proportions was lowest (0.004) associated with survival of 0.88 when compared to the fitted research-capture age structure, and lowest (0.003) associated with survival of 0.90 when compared to the fitted reconstruction age structure (Figure 4.8.5, Table 4.8.2). Across the range of modeled male survival rates, estimated difference between female and males ages ranged from 1.8 to 4.9 for mean age and ranged from 2 to 5 for median age (Table 4.8.2). Male survival rates corresponding most closely to field estimates of age difference were 0.91 for the mean age and 0.90 to 0.91 for the median. Finally, comparing model-predicted population sex ratio to that obtained from the ecosystem-wide DNA mark-recapture study conducted in 2004 (Kendall et al. 2009), the male survival rates corresponding most closely were 0.88 to 0.89.

Among all of these comparisons of field data to population modeling, we found little evidence that male survival rates were close to the lower estimates, derived by assuming all unknown-fate bears had died. Instead, evidence favored rates at the higher end of our estimated rates, obtained from censoring individuals whose fate was unknown, 0.88 to 0.91. Using the mean value within this range, we conclude that 0.895 is our best point estimate for independent male survival in the NCDE during 2004–2013, a rate 0.052 lower than the estimated survival rate for independent females. This estimate is slightly higher than the lower estimates of subadult (0.887 [2002–2011 estimate]) and adult (0.881 [1983–2001]) male survival in the GYE obtained when bears with unknown fates were assumed dead, and well below the higher estimates of subadult (0.950 [1983–2001]) and adult (0.948 [2002–2011]) survival obtained when bears with unknown fates were censored (Interagency Grizzly Bear Study Team 2012). We, therefore, used a male survival estimate of 0.895 in all subsequent population modeling in RISKMAN reported below.

Table 4.8.2. Comparisons of field-derived population age characteristics and sex ratio to those derived using RISKMAN population modeling. Model inputs were observed vital rate estimates (cub, yearling, and independent [≥2 years old] female survival; recruitment) and varying levels of independent male survival (within the estimated range) for grizzly bears in the NCDE. Highlighted values correspond most closely with field observations.

Method		Mean age			Median age			Sex ratio (F:M)	Age structure fit[a]	
		Female	Male	Difference	Female	Male	Difference		Capture	Reconstruction
Field Data										
Research-capture	Raw data	9.0	7.2	1.8	7.0	5.0	2	NA	NA	NA
	Fitted	9.3	7.4	1.8	7.0	6.0	1	NA	0.000	0.006
Population reconstruction	Raw data	9.0	8.5	0.5	8.0	6.0	2	NA	NA	NA
	Fitted	9.2	8.0	1.2	7.5	7.0	0.5	NA	0.006	0.000
DNA population estimation[b]	Model	NA	NA	NA	NA	NA	NA	0.62	NA	NA
RISKMAN modeling										
Male survival = 0.91	Model	10.6	8.9	1.8	9.0	7.0	2	0.58	0.010	0.005
Male survival = 0.90	Model	10.6	8.4	2.2	9.0	7.0	2	0.59	0.007	0.003
Male survival = 0.89	Model	10.6	8.1	2.6	9.0	6.0	3	0.61	0.005	0.004
Male survival = 0.88	Model	10.6	7.7	2.9	9.0	6.0	3	0.63	0.004	0.006
Male survival = 0.87	Model	10.6	7.3	3.3	9.0	6.0	3	0.64	0.005	0.008
Male survival = 0.86	Model	10.6	7.0	3.6	9.0	5.0	4	0.65	0.006	0.011
Male survival = 0.85	Model	10.6	6.7	3.9	9.0	5.0	4	0.67	0.009	0.013
Male survival = 0.84	Model	10.6	6.5	4.2	9.0	5.0	4	0.68	0.011	0.016
Male survival = 0.83	Model	10.6	6.2	4.4	9.0	5.0	4	0.69	0.013	0.018
Male survival = 0.82	Model	10.6	6.0	4.7	9.0	5.0	4	0.70	0.016	0.021
Male survival = 0.81	Model	10.6	5.8	4.9	9.0	4.0	5	0.71	0.018	0.023

[a] Value corresponds to the standard deviation of the mean difference between the proportion estimated using population reconstruction and the proportion estimated for each model, by age. Values closer to zero signify better fit. For reference, values for the female fit were 0.011 and 0.008, for the research capture and population reconstruction comparisons, respectively.

[b] Sex ratio obtained from DNA mark-recapture estimate of total population size in the NCDE (Kendall et al. 2009).
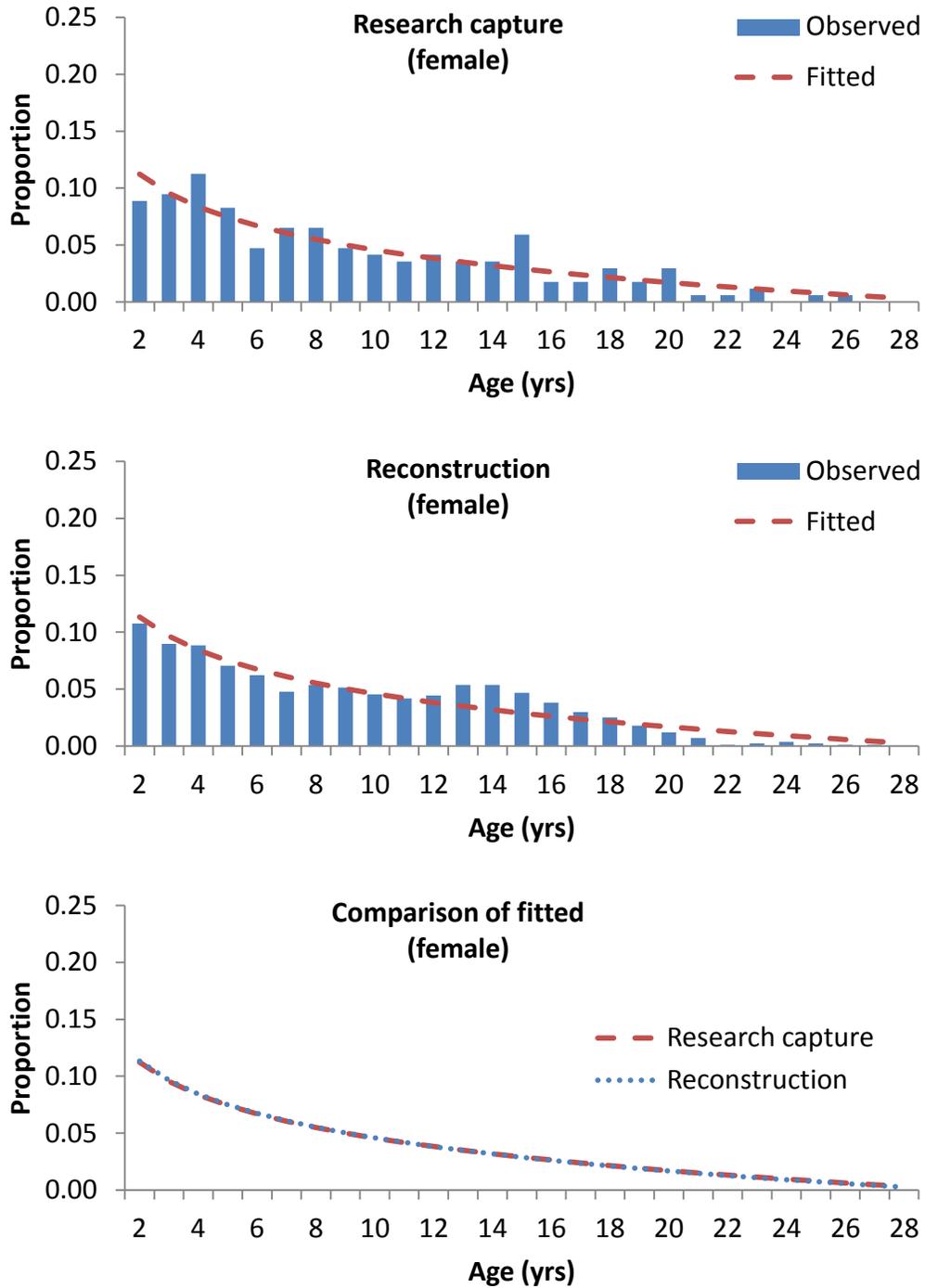
Figure 4.8.1. Observed and fitted age structure of independent (≥2 years old) female grizzly bears based on field data, NCDE. The research capture sample involved 169 captures of 129 females during 2002–2014 (top, bottom) and the population reconstruction sample involved 195 females known to be alive within 836 bear-years during 2004–2010 (center, bottom).
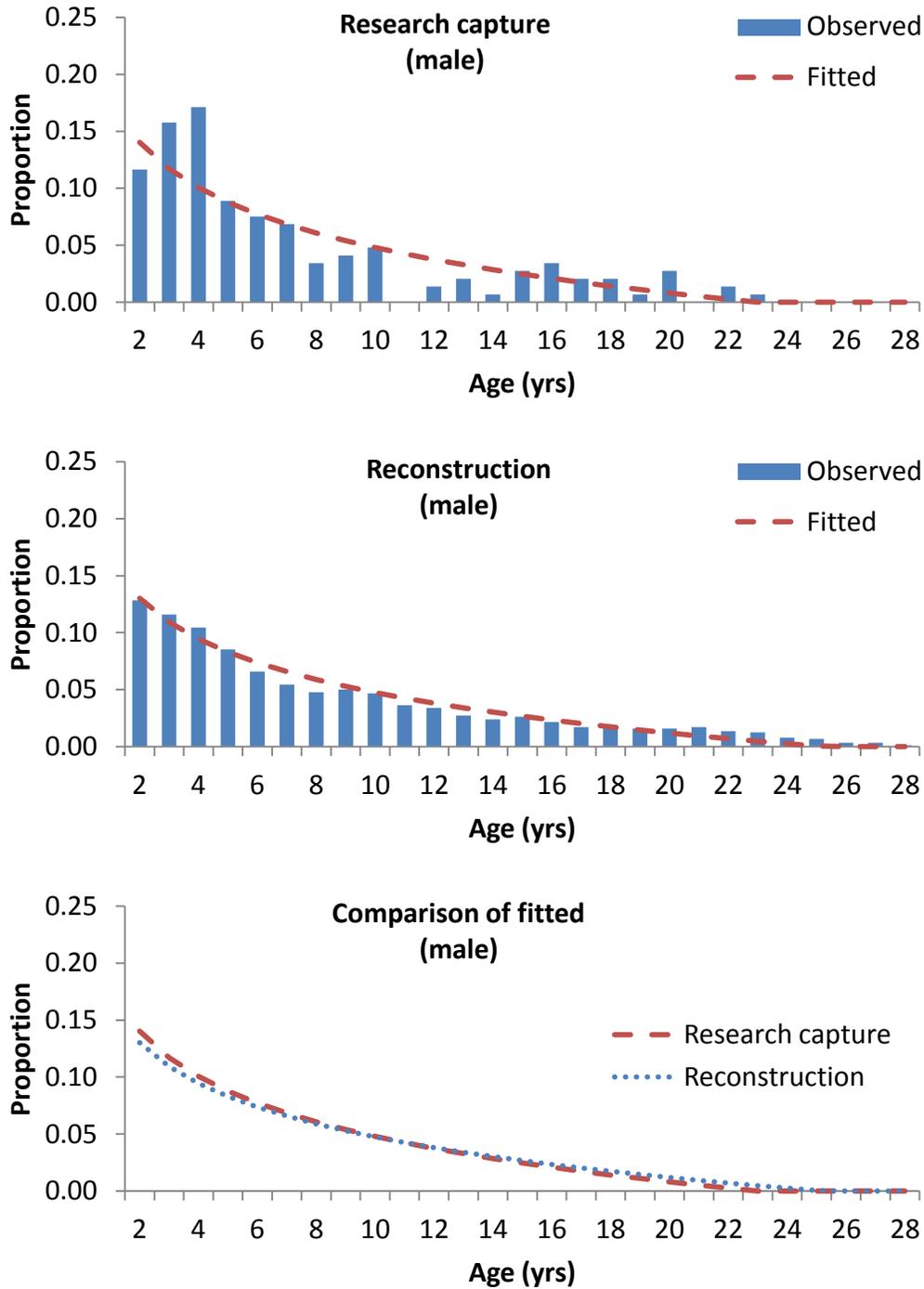
Figure 4.8.2. Observed and fitted age structure of independent (≥2 years old) male grizzly bears based on field data, NCDE. The research capture sample involved 146 captures of 125 males during 2002–2014 (top, bottom) and the population reconstruction sample involved 212 males known to be alive within 880 bear-years during 2004–2010 (center, bottom).
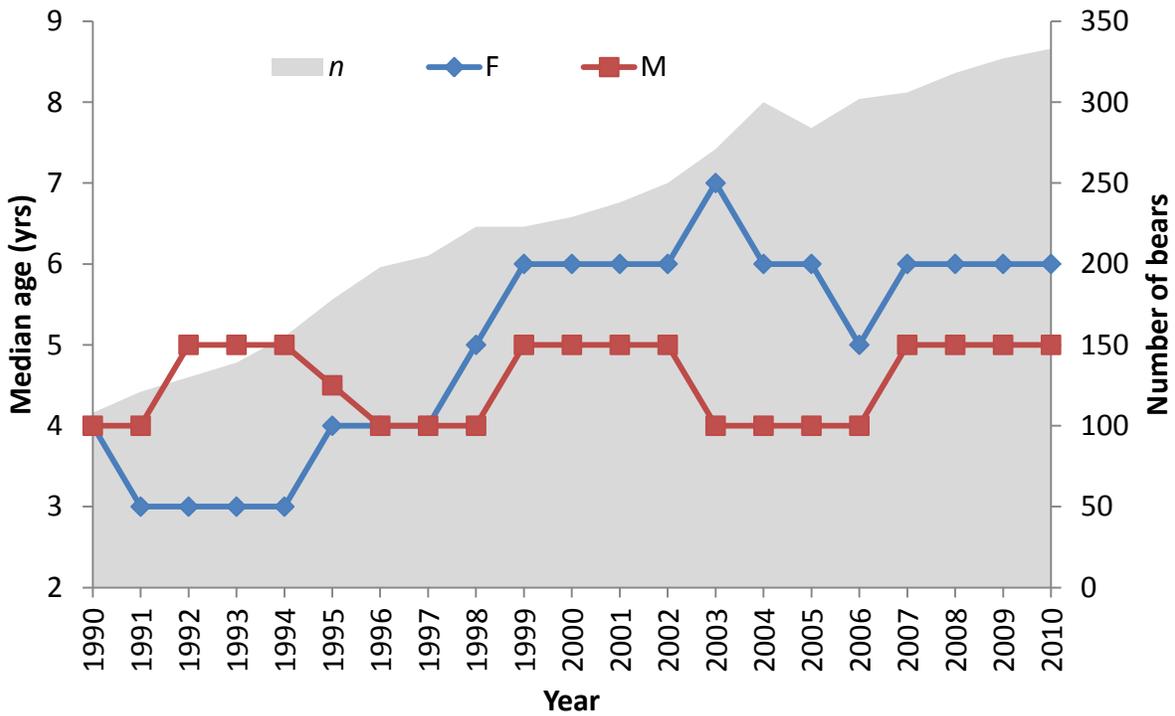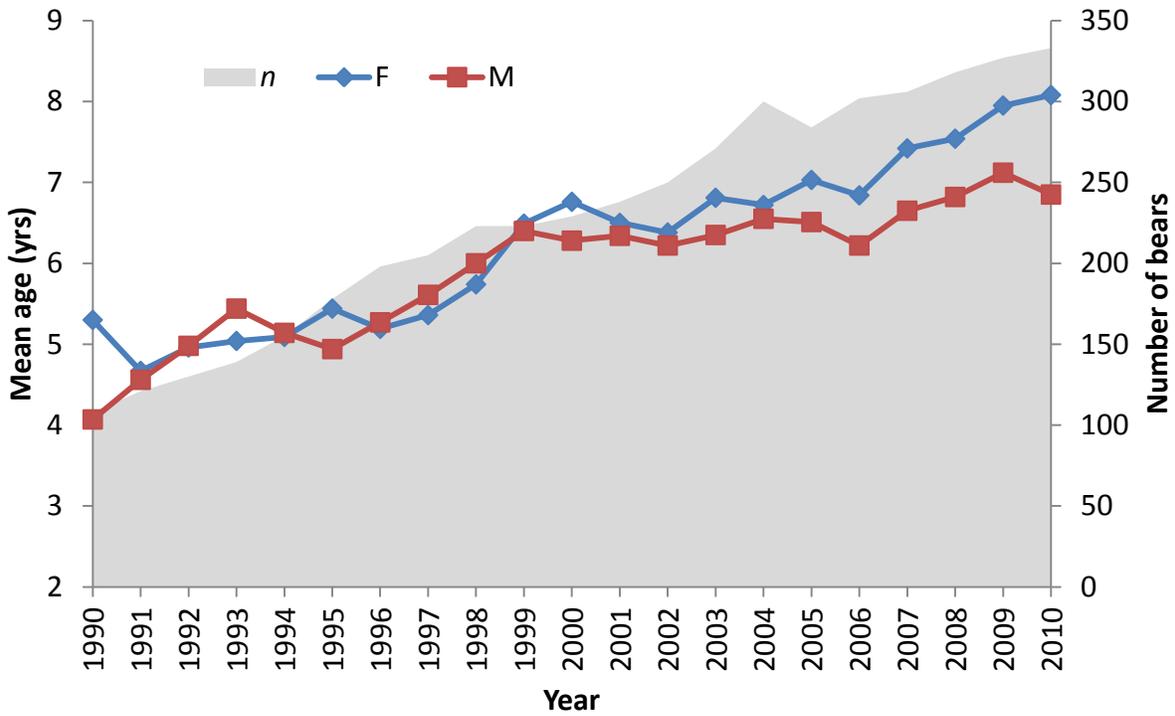
Figure 4.8.3. Mean (top) and median (bottom) ages of independent (≥2 years old) grizzly bears known to be alive, by year, NCDE, 1990–2010.
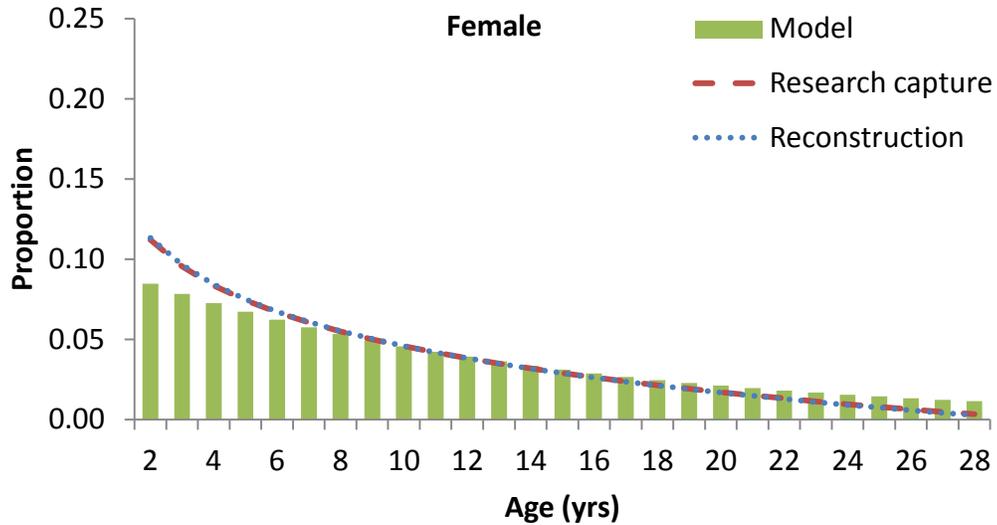
Figure 4.8.4. Comparison of RISKMAN model-predicted stable-age distribution to field-observed age structure for female grizzly bears in the NCDE, 2004–2014. Independent (≥2 years old) female survival was set at 0.947 for RISKMAN modeling, which was the mean value between the estimates obtained when unknown-fate bears were censored (0.951) and assumed dead (0.943). Resulting female age structure remained static with varying inputs for independent male survival. Field observed estimates were based on research capture during 2002–2014 and population reconstruction for bears known alive during 2004–2010.
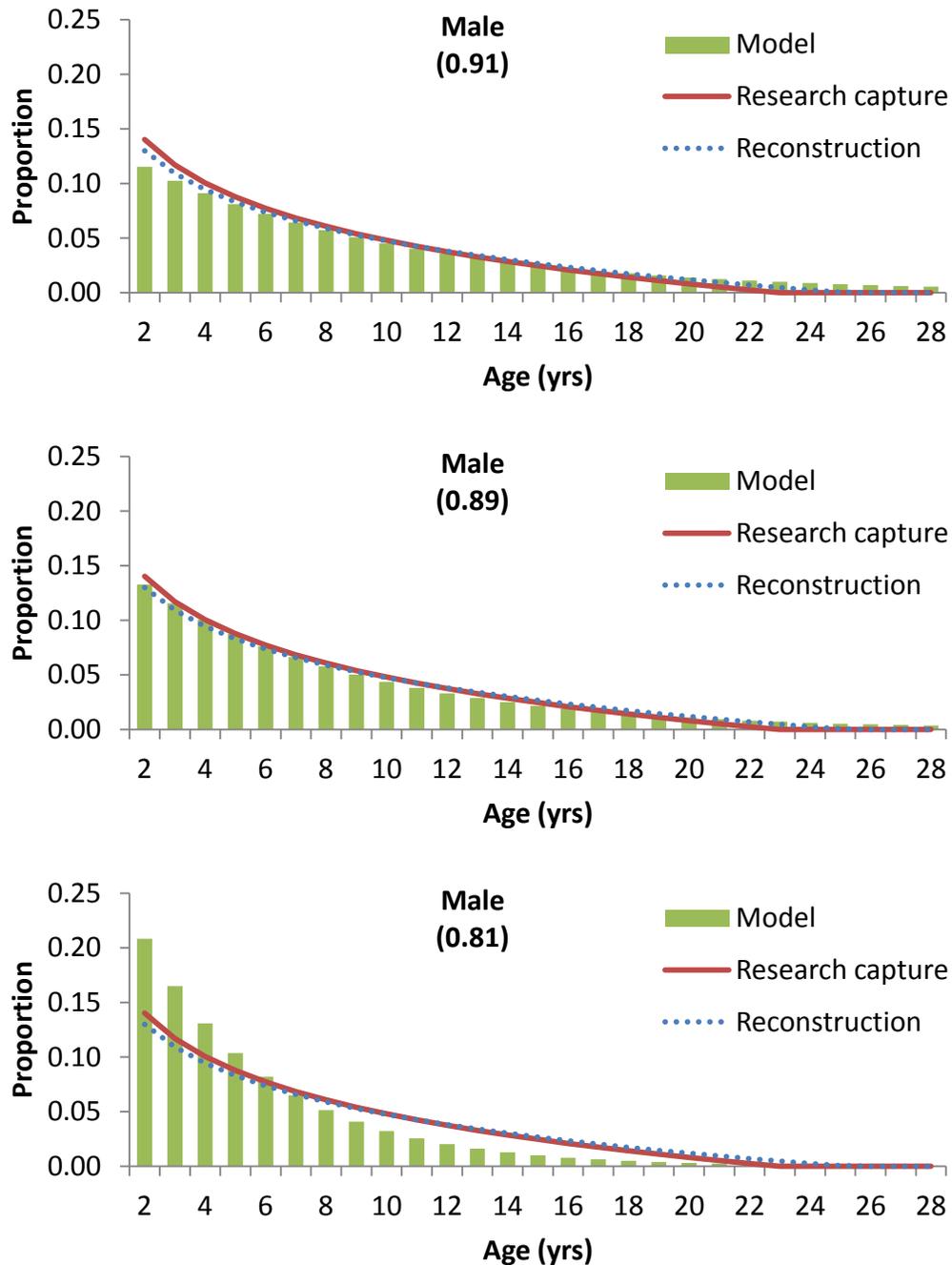
Figure 4.8.5. Comparison of RISKMAN model-predicted stable-age distribution to field-observed age structure for male grizzly bears, with varying levels of independent (≥2 years old) male survival used in RISKMAN modeling, NCDE, 2004–2014. Independent male survival rates depicted represent: the estimate when unknown-fate bears were censored (0.91, top); the estimate when unknown-fate bears were assumed dead (0.81, bottom); and the estimate between these extremes with the best fit to the field estimates (0.89, center). Independent female survival was set at 0.947. Field observed estimates were based on research capture during 2002–2014 and population reconstruction for bears known alive during 2004–2010.

4.9 Population Trajectory

The ultimate goal of this monitoring program is to estimate population trend. Here, we report the estimated population growth rate of the NCDE grizzly bear population, based on the vital rates observed and reported in the Sections 4.5 through 4.8.

Methods

To estimate population trajectory, we used two approaches. The first approach was a deterministic life-table analysis, which involved point estimates of vital rates and did not incorporate uncertainty. To compute the deterministic asymptotic rate of population growth (λ) during the study period, we created a standard, dynamic life table and solved iteratively for r (i.e., the intrinsic rate of growth), using the PopTools 3.2 add-in (www.poptools.org) for Microsoft Excel 2007 (Microsoft, Redmond, Washington). This is a female-only rate. We estimated λ using the three point estimates of independent female survival: (1) maximum (0.951), obtained when unknown-fate females were censured; (2) minimum (0.943), obtained when unknown-fate females were assumed dead; and (3) the mean of those two estimates (0.947).

The second approach was individual-based, stochastic population modeling, in which each simulation resulted in a potential population trajectory based on vital rates and the uncertainty associated with each vital rate. This approach allows for the inclusion of the male segment of the population. Using estimated recruitment rates, dependent bear survival rates, and independent bear survival rates for both females and males, we used RISKMAN to stochastically model population growth. We ran 2,000 10-year simulations (i.e., runs), corresponding to the period 2004–2014. We used 28 age classes corresponding to the oldest observed age; set the minimum age of reproduction at 4 years; set the maximum age of reproduction at 28 years; and employed the annual model because all of our vital rates were annual estimates. Input parameters were as shown in Table 4.8.1. Simulations started with a stable age distribution based on observed vital rates.

Results

Based on the standard, dynamic life table analysis, our estimate of λ was 1.023, corresponding with the mean rate of independent female survival. The λ estimate was 1.027 using the independent female survival rate obtained when females with unknown fates were censured, and the λ estimate was 1.020 using the independent female survival rate obtained when females with unknown fates were assumed dead.

Based on RISKMAN modeling of observed vital rates of the NCDE grizzly bear population during 2004–2014 and an initial population size of 765 in 2004 (Kendall et al. 2009), model output provided strong evidence for positive population growth during this period. Equivalent to the λ estimate obtained from life table analysis, the geometric mean population growth rate was 1.023. The median estimated population size was 855 bears at 5 years and 960 bears at 10 years (Figure 4.9.1). The upper and lower bounds of the 95th percentile of population size were 773– 946 bears at year 5 and 837–1,089 bears at year 10. Annual changes in the lower bound were consistent with a growth rate of 1.015, while annual changes in the upper bound were consistent with a growth rate of 1.029. Defining population decline as ending population size <95% of the initial population (727 bears), we found that only 0.2% of runs resulted in population decline at 5 years and 0.05% of runs resulted in population decline at 10 years.
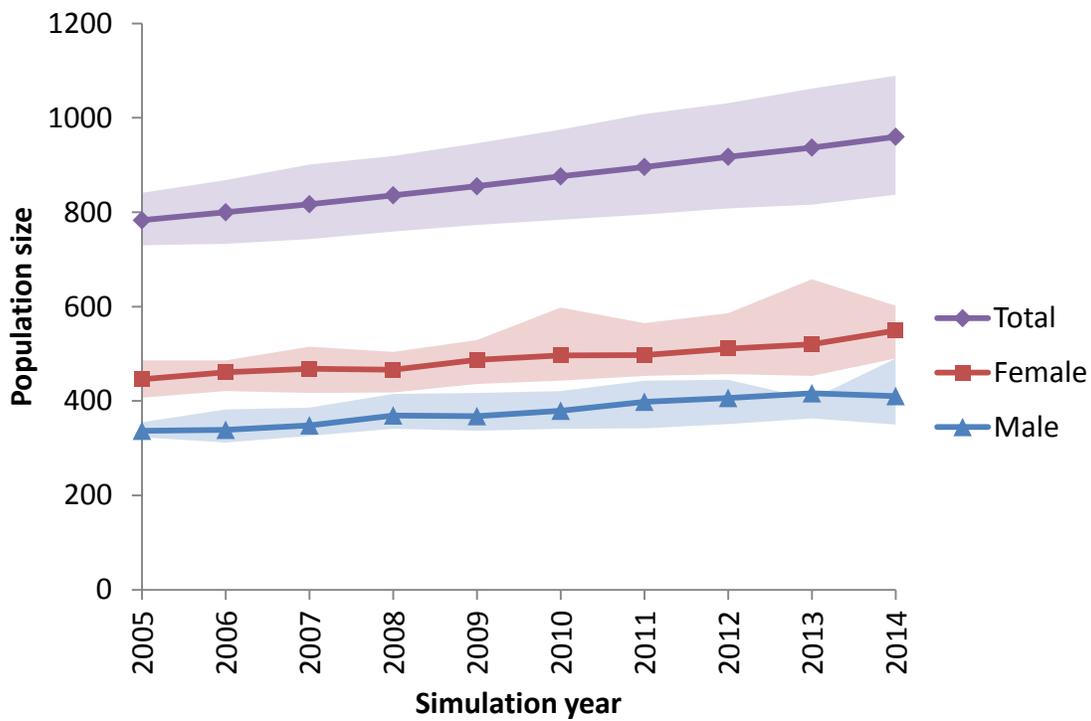
Figure 4.9.1.   Median and 95th percentile of population estimates obtained using 2000 RISKMAN simulations, based on observed grizzly bear vital rates during 2004–2014, and an initial population size of 765 in 2004 (Kendall et al. 2009).

4.10 Simulated Population Trajectory under Variable Independent Survival Rates

Along with the protection of habitat, the careful limitation of grizzly bear mortality, especially that of adult females, has been responsible for the growth of the NCDE population. Continued monitoring of, and limitations to, independent bear mortality is necessary to ensure the long-term persistence of this grizzly bear population, and these goals were put forth in the MFWP Grizzly Bear Management Plan for Western Montana (Dood et al. 2006). The Draft Conservation Strategy (USFWS 2013) included specific demographic standards that were tied to population viability. These standards were based, in part, on previous estimates of NCDE population parameters (Mace et al. 2012) and population analyses using those parameters (USFWS 2013 [Appendix 2]). The goal for this section was to update these analyses based on the vital rate estimates for 2004–2014. Specifically, we sought to estimate minimum sustainable survival rates for independent female and male bears, assuming observed rates of recruitment and dependent bear survival. For our analyses, we defined sustainable survival rates (and by extension, sustainable mortality thresholds, Section 4.11) as those that result in a stable-to-growing population trajectory, if maintained for an extended period, such as 10 years.

Methods

We ran a series of deterministic and stochastic population models to simulate population trajectory under varying levels of independent female and male survival, with observed rates for recruitment and dependent bear survival. Our goal was to incrementally decrease independent bear survival rates to evaluate when population parameters signaled stabilization of population growth and ultimately population decline (Table 4.10.1). First, using standard, dynamic life table analysis, we obtained a deterministic estimate of the asymptotic rate of population growth (λ), based on observed rates of recruitment, cub survival, and yearling survival (as applied to females only) and varying rates of independent female survival (ranging from 0.945 to 0.900 by increments of 0.005).

Second, using the RISKMAN program, we ran a series of stochastic population models to simulate two different management scenarios: (1) decreased survival of both independent females and males; and (2) decreased survival of independent males only. For each model, we ran 2000 10-year simulations (i.e., runs). We used 28 age classes corresponding to the oldest observed age; set the minimum age of reproduction at 4 years; set the maximum age of reproduction at 28 years; and employed the annual model because all of our vital rates were annual estimates. We input observed reproductive and juvenile survival rates as shown in Table 4.8.1. We ran these sets of models with 3 different initial population sizes (500, 765, and 1000) to evaluate the effect on results. For the scenario of increased

female and male mortality, with females as the focal sex, we ran models with independent female survival ranging from 0.945 to 0.900, by increments of 0.005. This equated to a ratio of modeled to observed mortality of 0.94 to 1.89. In other words, at the extreme, we nearly doubled the observed mortality rate. Applying these same ratios, we varied independent male survival from 0.890 to 0.800, by increments of 0.01. For the scenario of increased male mortality only, we ran models with independent male survival ranging from 0.89 to 0.75, by increments of 0.01. We started all simulations with the stable age distribution derived from simulations with observed vital rates (Section 4.9), similar to our field estimates of NCDE grizzly bear population structure (Section 4.8). We evaluated sustainability of the various survival rates using criteria described in Table 4.10.1 and examined their effects on the age structure of the population.

Results

Static life table analysis, based on the female segment of the population only, indicated that independent female survival rates ≥0.920 were associated with λ values ≥1.00 (Figure 4.10.1). This result was obtained independent of population size.
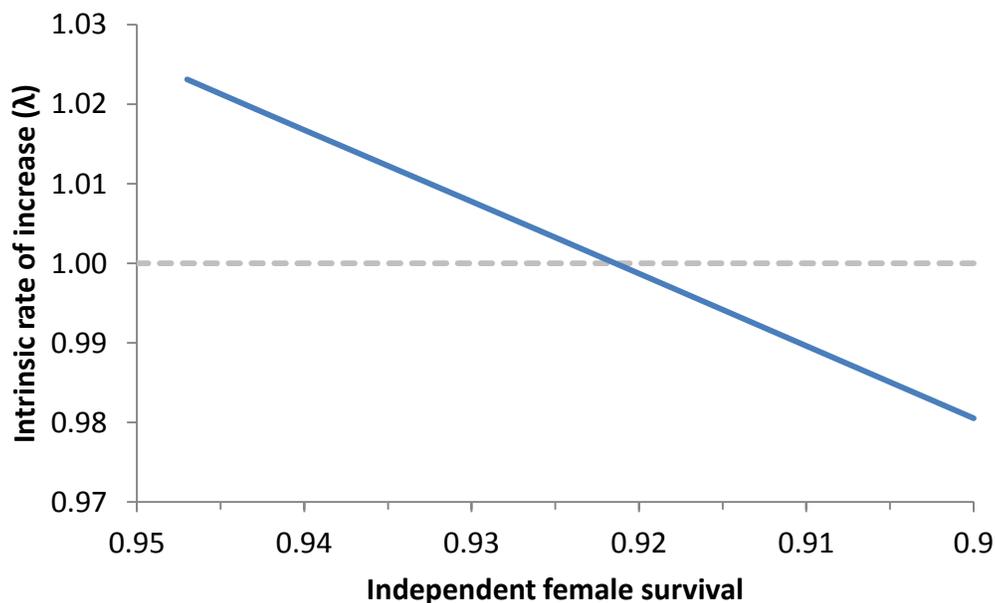
Figure 4.10.1. Relationship between the intrinsic rate of increase (λ) and decreasing rate of independent (≥2 years old) female survival (starting with the observed rate for the NCDE grizzly bear population during 2004–2014). Estimates were derived using standard, dynamic life table analyses utilizing observed rates of female recruitment and dependent female survival during 2004–2014.

Table 4.10.1. Population parameters, obtained from life table analysis using PopTools and from population modeling using RISKMAN, which can be used to evaluate sustainability of independent (≥2 years old) survival rates and/or estimate the number of sustainable independent bear mortalities for the NCDE grizzly bear population.

Parameter	PopTools (deterministic model)	RISKMAN (stochastic model)		
	Intrinsic rate of growth (λ)	Population size	Geometric mean growth rate	Probability of decline
Options		(1) Median (2) Lower bound of 95th percentile (3) Upper bound of 95th percentile	(1) Annual (2) Mean across years	(1) 95% of initial population size (2) 90% of initial population size (3) other options possible
Sustainability criteria	> 1 (growth) = 1 (stability) < 1 (decline)	(1) Maintain target population size (2) Maintain minimum population size	> 1 (growth) = 1 (stability) < 1 (decline)	Maintain ≤0.10 probability (other options possible)
Description	Rate of change from one year to the next of the female segment of the population. Estimates of λ are based on the survival and recruitment schedules of females only. For our analysis, we estimated λ using a static life table, however stochastic modeling of λ is also possible.	Ending population size for each year, taking into account reproduction and mortality	Rate of change from one year to the next for the entire population. Estimates are based on both female and male survival schedules. Mean growth rate is calculated across all of the individual runs in stochastic modeling. Range of estimate can also be estimated from 95th percentiles of population size.	Estimate is proportion of runs with ending population < x% of the initial population size. Estimates are calculated for each year of the simulation, allowing for evaluation of short-term and long term sustainability, depending on the number of years modeled.
Caveats	Depending on male survival rates, λ estimates >1 are possible, even when total population size is declining.		Growth rates >1 are possible, even when some runs indicate population decline.	

Using RISKMAN population modeling for the scenario of decreased female and male survival, model output indicated that estimates of mean population growth rate and probability of decline were largely unaffected by initial population size (Figure 4.10.2); detailed output is reported for models with the intermediate initial population size of 765. Model summaries indicated parameters associated with female survival rates of ≥0.930 and male survival rates of ≥0.860 were consistent with population stability or growth at both 5 and 10 years, whereas many parameters associated with female survival of 0.925 and male survival rate of 0.850 were consistent with population decline (Table 4.10.2, Figure 4.10.3). At the latter survival rates, mean growth rate declined to 0.998 at 5 and 10 years; probability of decline increased to 0.23 at 5 years and 0.27 at 10 years; and median population size declined to 756 at 5 years and 758 at 10 years. Stronger evidence for population decline was evident when independent female and male survival rates were ≤0.920 and ≤0.840, respectively. Results were similar when initial population size was 500 and 1000, except that probability of decline first exceeded 0.10 (i.e., 0.14) at a female survival rate of 0.930 and male survival rate of 0.860 when population size started at 500.

For the scenario of decreased male survival only, model output indicated that estimates of mean population growth rate were largely unaffected by initial population size, but probability of decline varied somewhat depending on initial population size (Figure 4.10.4). Again, detailed output is reported for models with the intermediate initial population size of 765. Parameters were consistent with population growth or stability when independent male survival rates were ≥0.800. Model summaries indicated parameters associated with male survival of 0.800 were largely consistent with population stability or growth, while many parameters associated with male survival of ≥0.790 were consistent with population decline (Table 4.10.3, Figure 4.10.5). Probability of decline at 5 years increased to 0.11 at male survival of 0.790; mean 5-year growth rate declined to 0.998 at male survival of 0.780; and median 5-year population size declined to 758 at male survival of 0.750. At lower rates of male survival, population parameters were consistent with population decline during the first 5–8 years of the simulations, but were consistent with growth by the end of the period. This occurred because the female survival rate used in these models was associated with a positive λ of 1.023. In fact, given enough years, all models would have eventually converged on this growth rate once a stable age distribution was achieved. Nonetheless, these results illustrate realistic numerical impacts of increased male mortality on bear population size in the short term.

Under this scenario of increased male-only mortality, we observed some potentially undesirable population characteristics at lower male survival rates, including significant reductions in mean male age and increases in proportion of males in the population (Table 4.10.3 and Figure 4.10.6). At a male survival rate of 0.800, a rate which was numerically sustainable in terms of population trajectory, mean

male age fell to 3.4 years compared to 7.8 years for females by year 10. Similarly, mean proportion of males in the population decreased from 0.43 to 0.36. By comparison, under the scenario of increased female and male survival, by year 10 mean male age was 4.9 years, mean female age was 7.7 years, and proportion of males in the population was 0.42 when the combined female and male survival rates were at the lowest sustainable levels (0.930 and 0.860, respectively; Table 4.10.2).

Although an estimated independent male survival rate of only 0.80 was sustainable when female survival was maintained at our observed rate of 0.947, higher male rates were necessary for sustainability when female survival rates were lower (Figure 4.10.7). Irrespective of female survival rates, mean age of males was low and proportion of females in the population was high when male survival was below 0.80. Under a scenario with any additional independent female mortality (i.e., if female survival drops below our observed rate of 0.947), male survival rates of 0.85 and above would be most likely to ensure continued population stability or growth and similar ratios of adult males in the population to those that would have been observed without the additional mortality. Similarly, under any scenario with additional male mortality, female survival rates of 0.930 and above would be most consistent with population stability or growth.
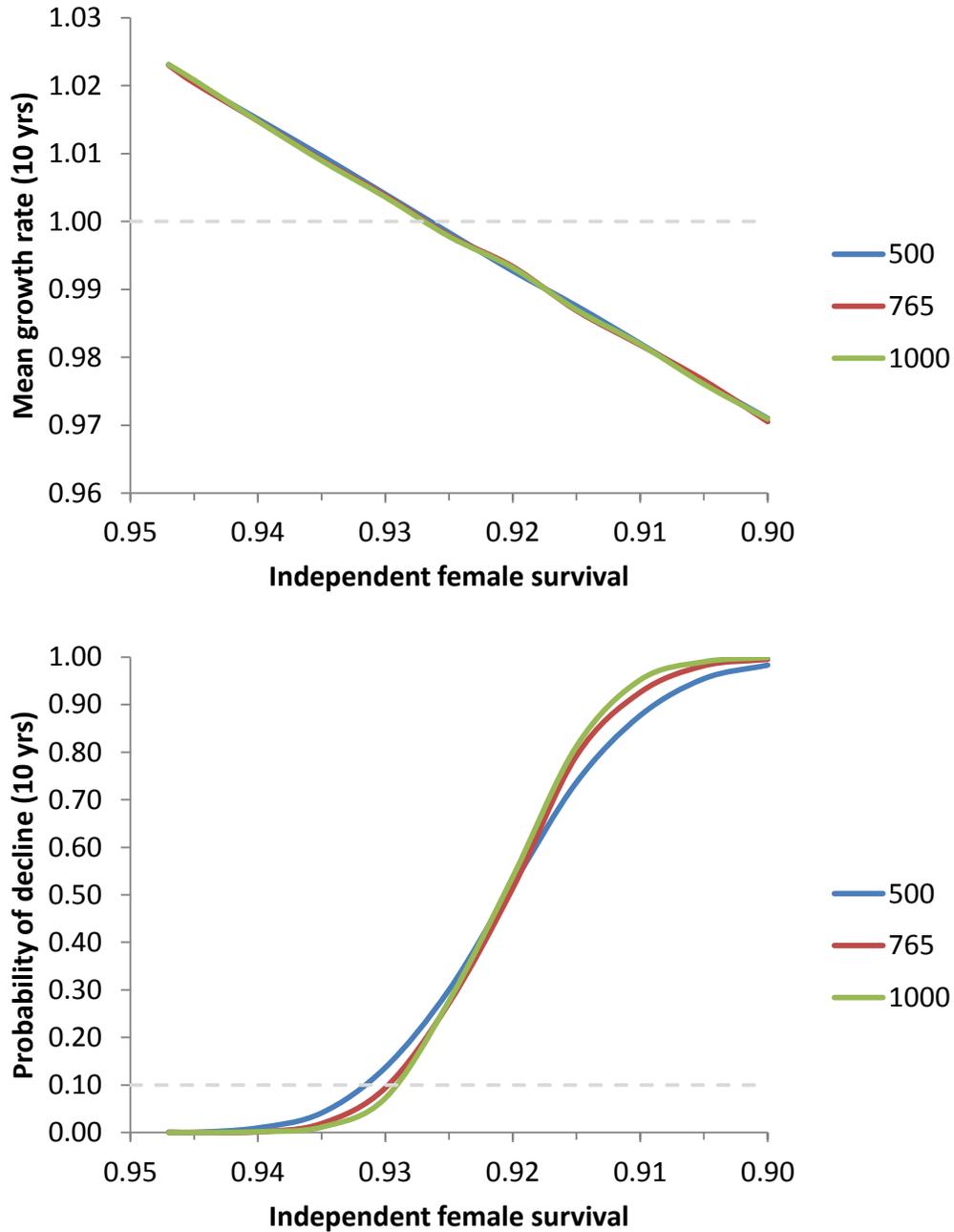
Figure 4.10.2. Relationships between simulated population parameters and initial population size for the scenario of decreasing rates of independent (≥2 years old) female and male survival (starting with observed rates for the NCDE grizzly bear population during 2004–2014). Simulations utilized observed recruitment rate, observed dependent bear survival rates, and an initial stable age distribution based on all observed vital rates during 2005–2014. Criteria for evaluating sustainability were: (top) a mean population growth rate at 10 years of ≥1.00; and (bottom) a probability of decline at 10 years of ≤0.10.
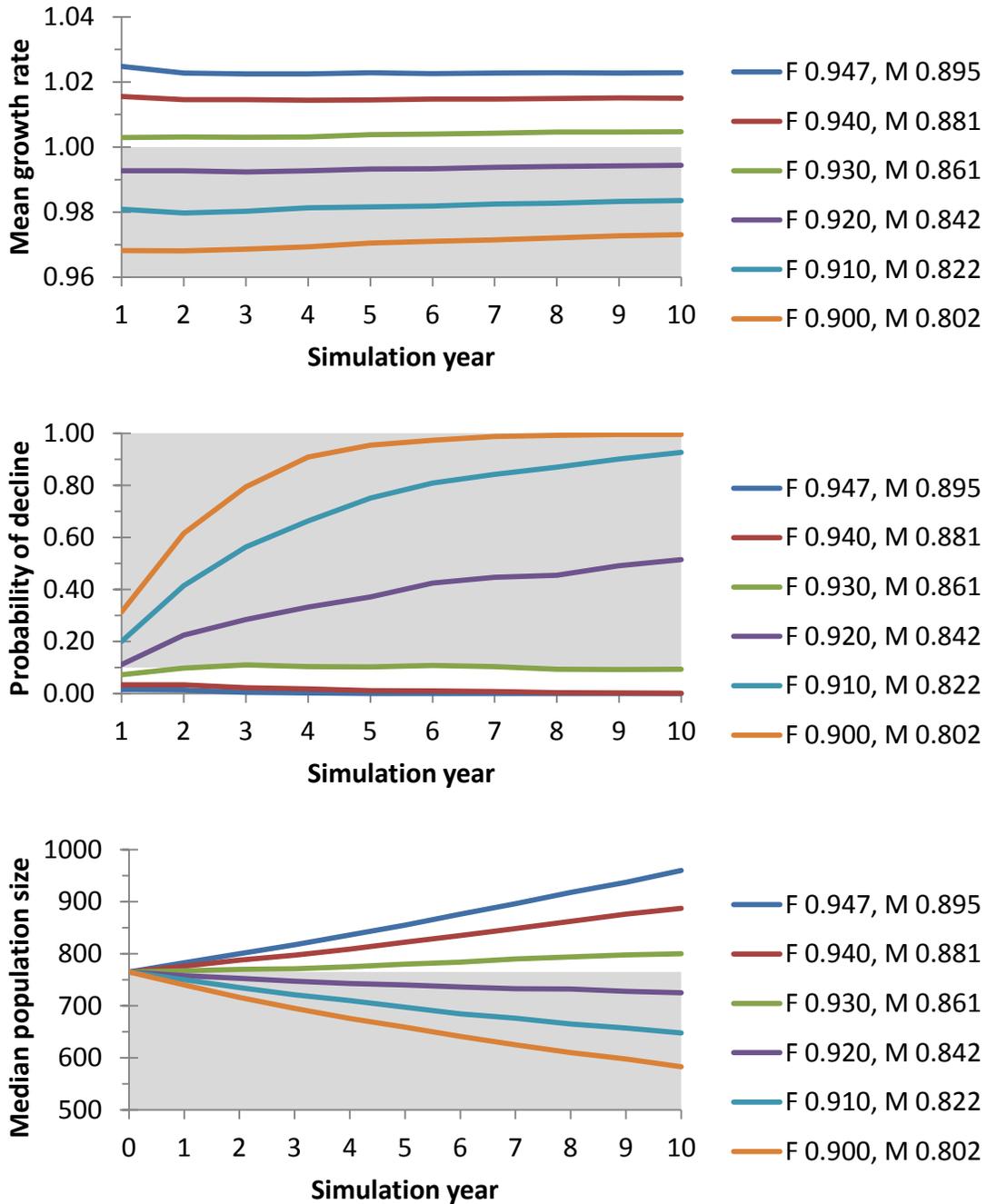
Figure 4.10.3. Results of stochastic population modeling, by simulation year, under the scenario of decreasing rates of independent (≥2 years old) female and male survival (starting with rates observed in the NCDE during 2004–2014). Simulations utilized observed recruitment rate, observed dependent bear survival rates, and an initial stable age distribution based on all observed vital rates during 2005–2014. Criteria for evaluating sustainability were: (top) mean population growth rate of ≥1.00; (center) probability of decline ≤0.10; and (bottom) median population size above initial size. These results were obtained using an intermediate initial population size of 765 bears, but results were similar using initial population sizes of 500 and 1000 bears.

Table 4.10.2. Simulated population parameters for NCDE grizzly bears, assuming the scenario of additional female and male mortality (i.e., survival rates below observed rates obtained using radio-telemetry). Model results were derived using stochastic population modeling with RISKMAN software, based on observed recruitment rate, observed dependent bear survival rates, and varying rates of independent (≥2 years old) female and male survival. Models began with the stable age distribution derived from observed vital rates. Three initial population sizes were used: 500, 765, and 1000 bears. Parameters consistent with population growth or stability were: mean population growth rate of ≥1.00; probability of decline ≤0.10; and median population size ≥ initial population size. Shaded values signify when criteria were consistent with declining population trajectory. The table presents all models for the intermediate initial population size of 765 (Kendall et al. 2009) and the first model(s) with criteria consistent with declining trajectory for the initial population sizes of 500 and 1000.

Values entered into model			Model output										
Initial N[a]	Independent survival rate		Geometric mean growth rate		Probability of decline[b]		Final N[a] (median)		Final N[a] (lower 95th percentile)		Mean age (10 yrs)		Proportion male (10 yrs)
	Female	Male	5 yrs	10 yrs	5 yrs	10 yrs	5 yrs	10 yrs	5 yrs	10 yrs	Female	Male	
765	0.947	0.895	1.023	1.023	<0.01	<0.01	855	960	768	838	7.8	5.3	0.43
765	0.945	0.890	1.021	1.020	<0.01	<0.01	847	938	762	815	7.8	5.3	0.43
765	0.940	0.880	1.015	1.015	0.01	<0.01	822	887	738	775	7.8	5.2	0.42
765	0.935	0.870	1.009	1.009	0.04	0.02	801	843	715	732	7.7	5.0	0.42
765	0.930	0.860	1.004	1.004	0.10	0.09	780	800	696	692	7.7	4.9	0.42
765	0.925	0.850	0.998	0.998	0.23	0.27	756	758	675	655	7.7	4.7	0.41
765	0.920	0.840	0.992	0.993	0.37	0.51	740	725	658	613	7.6	4.6	0.41
765	0.915	0.830	0.986	0.987	0.60	0.79	716	685	634	584	7.6	4.5	0.41
765	0.910	0.820	0.981	0.982	0.75	0.93	697	648	617	550	7.6	4.4	0.40
765	0.905	0.810	0.976	0.977	0.87	0.98	678	615	599	514	7.6	4.2	0.40
765	0.900	0.800	0.969	0.971	0.95	1.00	659	583	583	491	7.5	4.1	0.39
500	0.930	0.860	1.004	1.004	0.14	0.14	509	525	447	438	7.7	4.8	0.42
500	0.925	0.850	0.998	0.998	0.27	0.30	495	497	443	416	7.7	4.7	0.41
1000	0.925	0.850	0.997	0.998	0.23	0.28	990	992	888	861	7.7	4.7	0.41

[a] Population size.
[b] Decline defined as final N <95% of initial N.
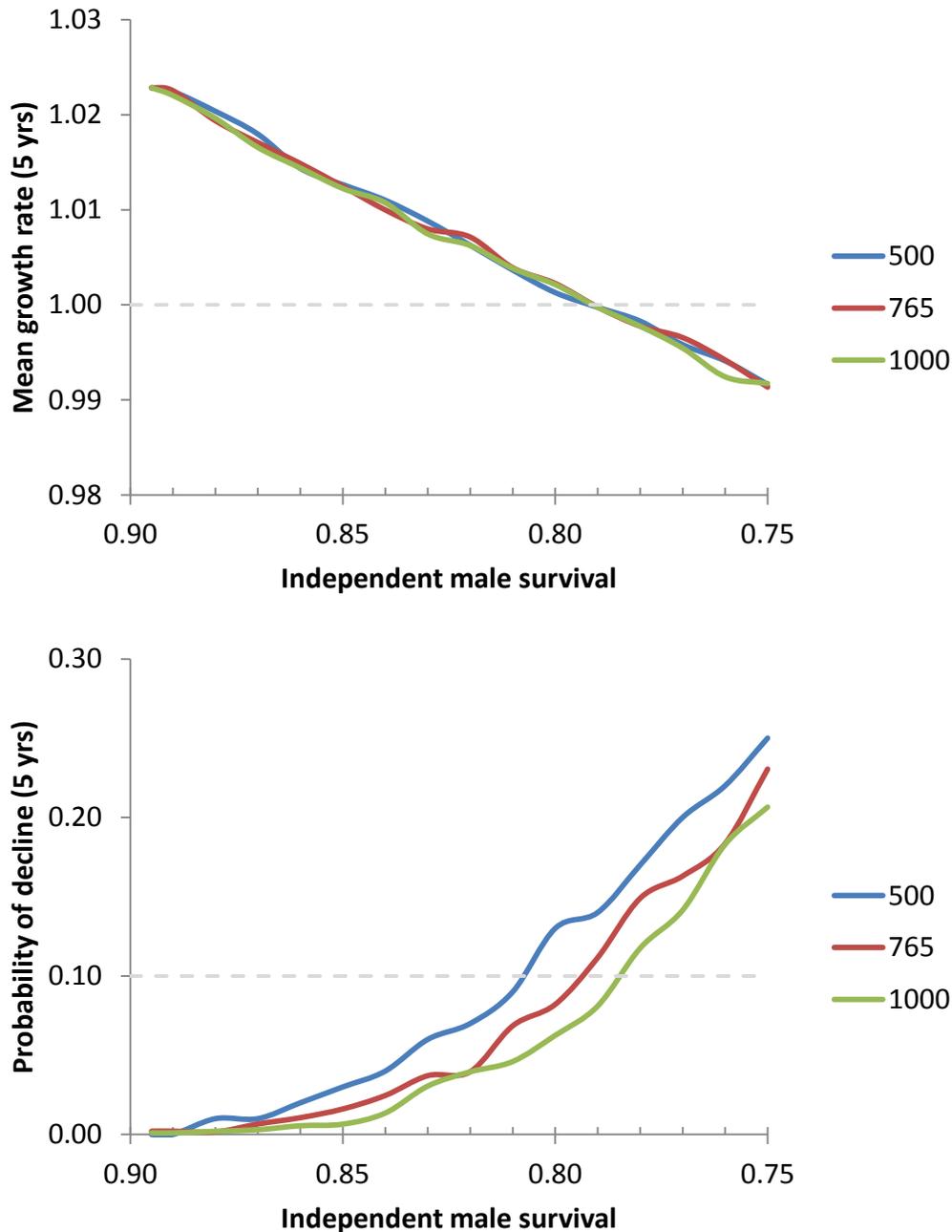
Figure 4.10.4. Relationships between simulated population parameters and initial population size for the scenario of decreasing rates of independent (≥2 years old) male survival only (starting with the observed rate for the NCDE grizzly bear population during 2004–2014). Simulations utilized observed recruitment rate, observed dependent bear survival rates, observed independent female survival rate, and an initial stable age distribution based on all observed vital rates during 2005–2014. Criteria for evaluating sustainability were: (top) a mean population growth rate at 5 years of ≥1.00; and (bottom) a probability of decline at 5 years of ≤0.10.
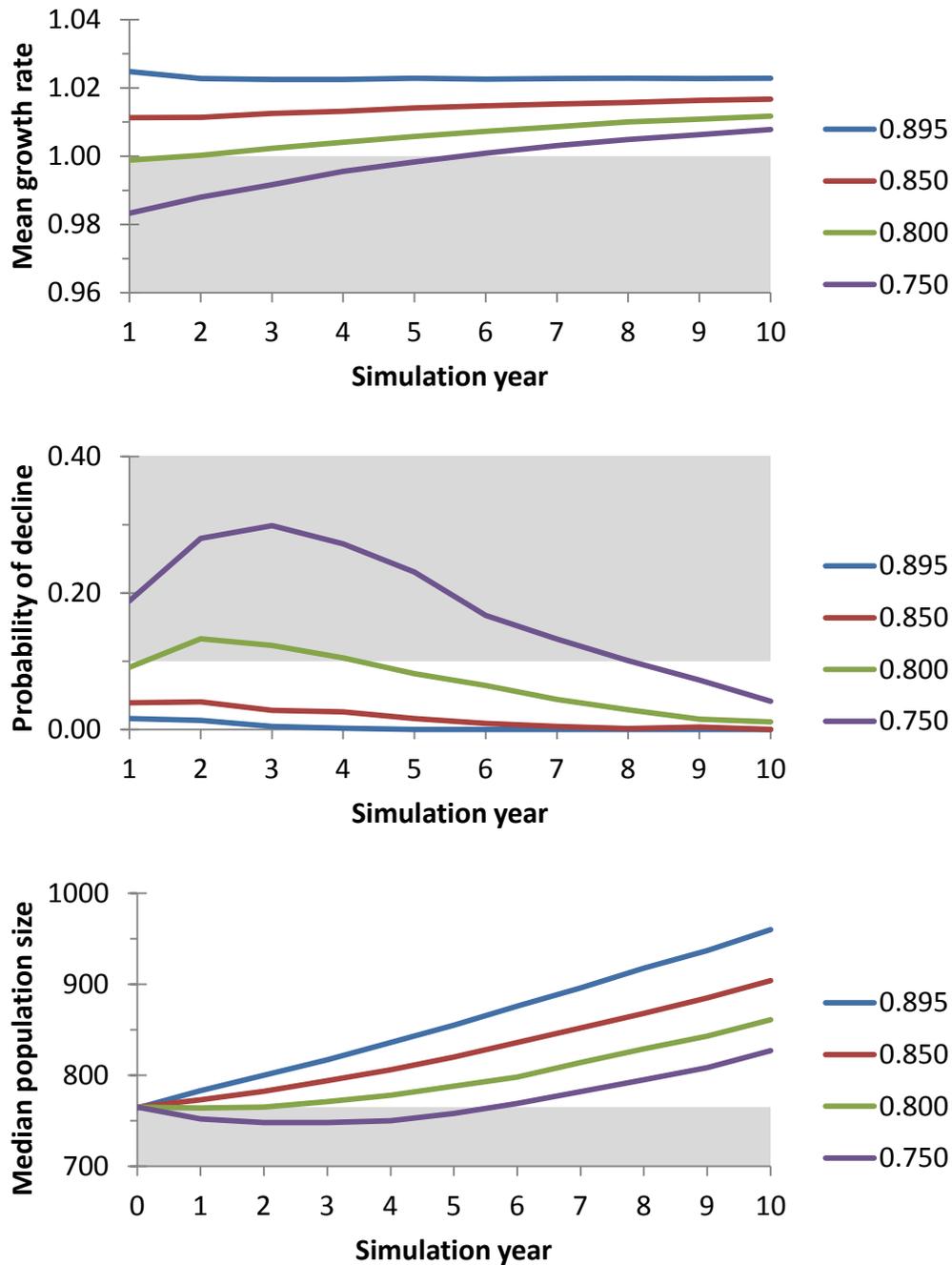
Figure 4.10.5. Results of stochastic population modeling, by simulation year, under the scenario of decreasing rates of independent (≥2 years old) male survival (starting with the rate observed in the NCDE during 2004–2014). Simulations utilized observed recruitment rate, observed dependent bear survival rates, observed independent female survival rate, and an initial stable age distribution based on all observed vital rates during 2005–2014. Criteria for evaluating sustainability were: (top) mean population growth rate of ≥1.00; (center) probability of decline ≤0.10; and (bottom) median population size above initial size. These results were obtained using an intermediate initial population size of 765 bears, but results were similar using initial population sizes of 500 and 1000 bears.

Table 4.10.3. Simulated population parameters for NCDE grizzly bears, assuming the scenario of additional male mortality only (i.e., survival rates below the observed rate obtained using radio-telemetry). Model results were derived using stochastic population modeling with RISKMAN software, based on observed recruitment rate, observed dependent bear survival rates, observed independent (≥2 years old) female survival rate, and varying rates of independent male survival. Models began with the stable age distribution derived from observed vital rates. Three initial population sizes were used: 500, 765, and 1000 bears. Parameters consistent with population growth or stability were: mean population growth rate of ≥1.00; probability of decline ≤0.10; and median population size ≥ initial population size. Shaded values signify when criteria were consistent with declining population trajectory. The table presents all models for the intermediate initial population size of 765 (Kendall et al. 2009) and the first models with criteria consistent with declining trajectory for the initial population sizes of 500 and 1000.

Values entered into model			Model output										
Initial N[a]	Independent survival rate		Geometric mean growth rate		Probability of decline[b]		Final N[a] (median)		Final N[a] (lower 95th percentile)		Mean age (10 yrs)		Proportion male (10 yrs)
	Female	Male	5 yrs	10 yrs	5 yrs	10 yrs	5 yrs	10 yrs	5 yrs	10 yrs	Female	Male	
765	0.947	0.830	1.008	1.010	0.04	<0.01	805	883	719	766	7.8	3.9	0.38
765	0.947	0.820	1.007	1.010	0.04	0.01	803	878	717	760	7.8	3.7	0.38
765	0.947	0.810	1.004	1.007	0.07	0.01	794	870	708	748	7.8	3.5	0.37
765	0.947	0.800	1.002	1.006	0.08	0.01	788	861	701	745	7.8	3.4	0.36
765	0.947	0.790	1.000	1.004	0.11	0.02	782	852	697	735	7.8	3.2	0.36
765	0.947	0.780	0.998	1.003	0.15	0.03	776	845	690	723	7.8	3.1	0.35
765	0.947	0.770	0.997	1.002	0.16	0.02	773	841	688	728	7.8	2.9	0.35
765	0.947	0.760	0.994	1.000	0.18	0.04	767	836	680	714	7.8	2.8	0.35
765	0.947	0.750	0.991	0.998	0.23	0.04	758	827	647	714	7.8	2.7	0.34
500	0.947	0.800	1.001	1.005	0.13	0.03	515	561	445	468	7.8	3.4	0.36
500	0.947	0.780	0.998	1.003	0.17	0.04	509	554	445	466	7.8	3.1	0.35
500	0.947	0.75	0.992	0.998	0.25	0.07	498	542	431	452	7.8	2.7	0.34
1000	0.947	0.78	0.998	1.003	0.12	0.01	1014	1106	917	973	7.8	3.1	0.35
1000	0.947	0.76	0.992	0.999	0.18	0.02	998	1089	890	952	7.8	2.8	0.34

[a] Population size.
[b] Decline defined as final N <95% of initial N.
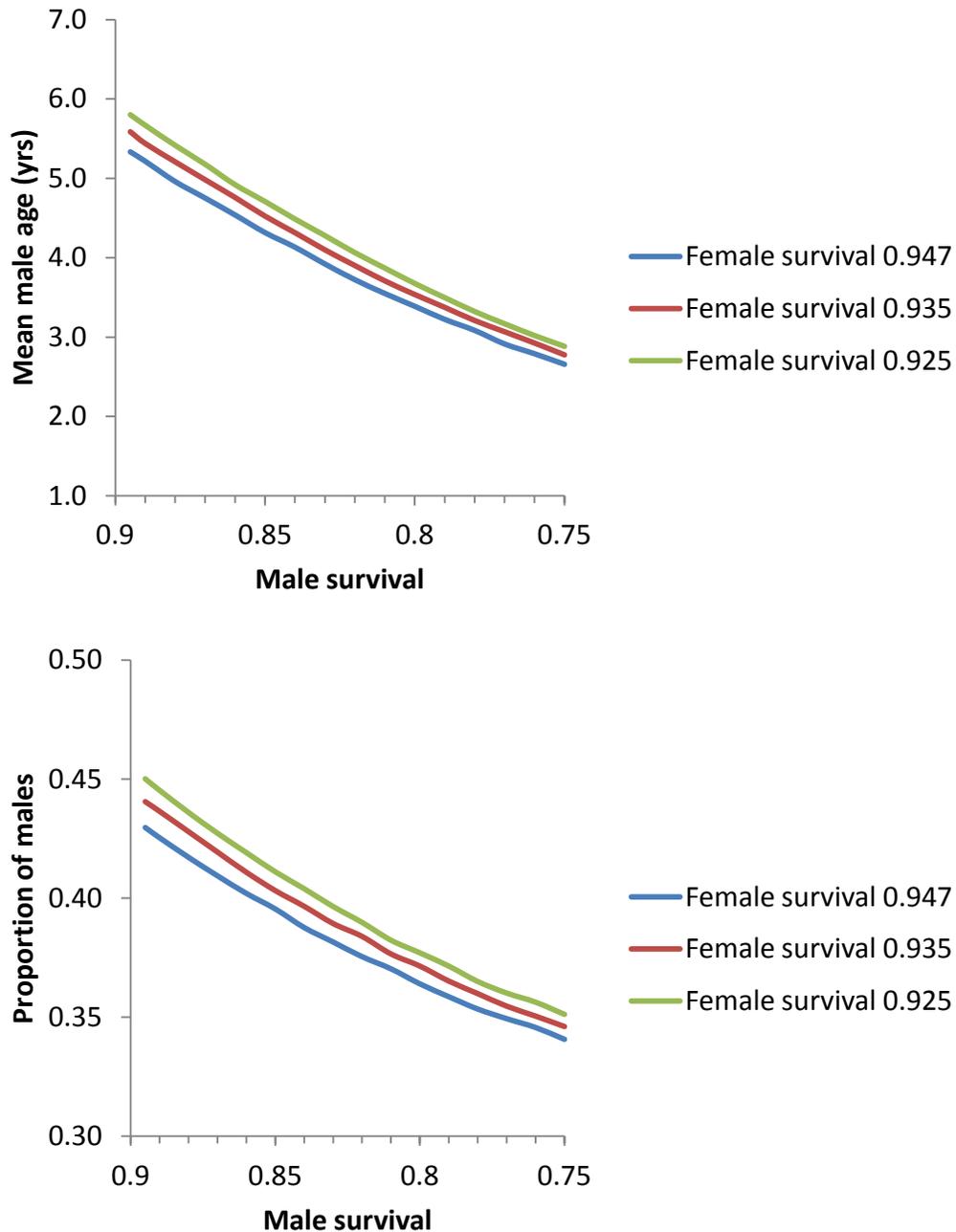
Figure 4.10.6. Relationships between characteristics of the male segment of the population and decreasing rates of independent (≥2 years old) male survival (starting with the observed rate for the NCDE grizzly bear population during 2004–2014), as a function of decreasing rates of independent female survival (also starting with the observed rate during 2004–2014). Simulations utilized observed recruitment rate, observed dependent bear survival rates, and an initial stable age distribution based on all observed vital rates during 2005–2014. Characteristics were: (top) mean male age at 10 years; and (bottom) proportion of males in the population at 10 years. These results were obtained using an intermediate initial population size of 765 bears, but results were similar using initial population sizes of
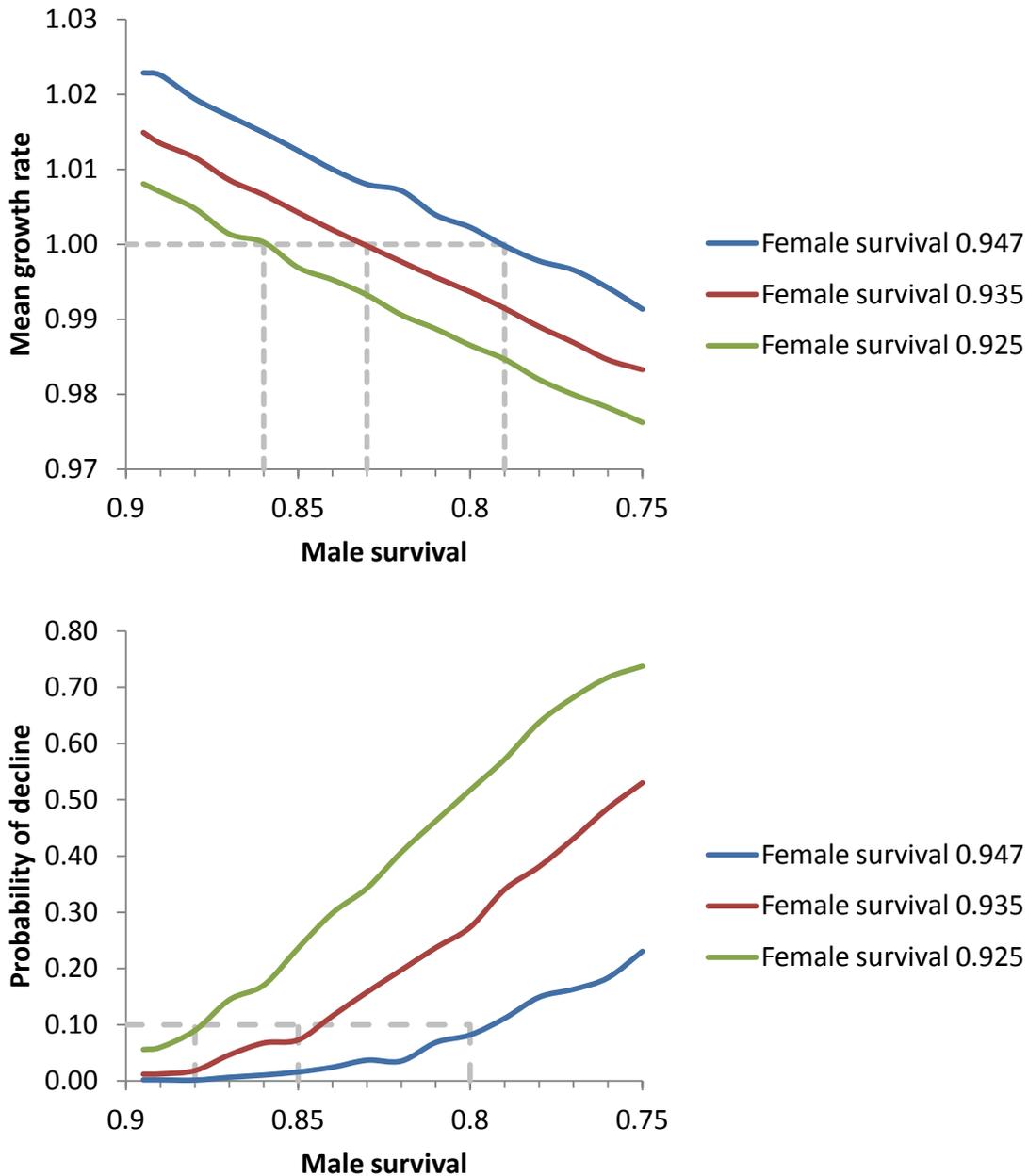
Figure 4.10.7. Relationships between simulated population parameters and decreasing rates of independent (≥2 years old) male survival (starting with the observed rate for the NCDE grizzly bear population during 2004–2014); as a function of decreasing rates of independent female survival (also starting with the observed rate during 2004–2014). Simulations utilized observed recruitment rate, observed dependent bear survival rates, and an initial stable age distribution based on all observed vital rates during 2005–2014. Criteria for evaluating sustainability were: (top) a mean population growth rate at 5 years of ≥1.00; and (bottom) a probability of decline at 5 years of ≤0.10. These results were obtained using an intermediate initial population size of 765 bears, but results were similar using initial population sizes of 500 and 1000 bears.

4.11 Estimation of Sustainable Mortality

An understanding of minimum sustainable survival rates is crucial for the long-term maintenance of the NCDE grizzly bear populations. However, this information is most useful for management of the population if it can be interpreted to estimate sustainable mortality rates. In the previous section, we estimated minimum independent female and male survival rates consistent with a stable or increasing trend in the grizzly bear population, for two different management scenarios. Given that there was little variation in these minimum survival rates, relative to bear population sizes ranging from 500 to 1000 bears, it would then be possible to estimate the number of mortalities that should be sustainable among independent female and male bears as a function of estimated population size. However, given the variety of methods used to estimate parameters (i.e., vital rates, population size, and total estimated independent bear mortality) and their uncertainty, direct application of these numbers as mortality thresholds requires additional evaluation.

In this section, we conduct further modeling and analyses, integrating the reported information on sustainable independent bear survival rates (Section 4.10), estimated population size (Section 3), and total estimated independent bear mortality (Section 4.4), to evaluate and adjust the number of sustainable independent bear mortalities. Our goals are to provide information to managers to help guide future population management decisions and to establish protocols for setting sustainable mortality thresholds in the future.

Methods

We calculated potential mortality thresholds, as a function of estimated population size, for grizzly bears in the NCDE under two management scenarios, based on: (1) the lowest sustainable survival rates obtained using stochastic population modeling with RISKMAN software, based on observed recruitment rate, observed dependent bear survival rates, and varying rates of independent female and male survival; and (2) proportions of independent female and male bears in the population based on the stable age distribution derived using observed rates (Table 4.11.1).

We used two methods to evaluate the calculated mortality thresholds, based on retrospective analyses integrating stochastic population modeling and the observed counts of estimated total mortality during 2004–2014 (Section 4.4). Our rationale was to simulate increased mortality of independent bears during this period, relative to our observed annual counts of total independent grizzly bears mortality, to determine if the calculated mortality thresholds were sustainable. The two methods differed in their assumptions. The first method assumed a known initial population size of 765 in 2004 and calculated

Table 4.11.1. Calculated mortality thresholds, as a function of estimated population size, for grizzly bears in the NCDE under two management scenarios. Estimates were based on: (1) the lowest sustainable survival rates obtained using stochastic population modeling with RISKMAN software, based on observed recruitment rate, observed dependent bear survival rates, and varying rates of independent (≥2 years old) female and male survival; and (2) proportions of independent female and male bears in the population based on the stable age distribution derived using observed rates.

| Estimated population size | Estimated mortality thresholds for independent bears[a] | | | | | |
| | Scenario of additional female and male mortality[a] | | | Scenario of additional male mortality only[b] | | |
	Female[b]	Male[c]	Total	Female[d]	Male[e]	Total
500	14	19	33	11	27	38
550	16	21	37	12	30	42
600	17	23	40	13	33	46
650	19	25	44	14	35	49
700	20	27	47	15	38	53
750	22	28	50	16	41	57
800	23	30	53	17	43	60
850	24	32	56	19	46	65
900	26	34	60	20	49	69
950	27	36	63	21	52	73
1000	29	38	67	22	54	76
1050	30	40	70	23	57	80
1100	32	42	74	24	60	84
1150	33	44	77	25	62	87
1200	35	46	81	26	65	91

[a] Thresholds were calculated, by sex, as proportion of independent bears in population × (1 − lowest sustainable survival rate) × N
[b] $0.41 \times 0.07 \times N$ or 2.87% of N
[c] $0.27 \times 0.14 \times N$ or 3.78% of N
[d] $0.41 \times 0.053 \times N$ or 2.17% of N
[e] $0.27 \times 0.20 \times N = 5.40\%$ of N

additional sustainable mortalities independent of observed numbers of mortalities. The second method did not assume any known population size, but estimated additional mortalities in direct proportion to observed mortalities.

For Method 1, we simulated population growth during 2004–2014 using all observed rates (Table 4.8.1) and an initial population size of 765 as estimated for 2004 (Kendall et al. 2009), but input additional annual mortalities of independent bears using the "hunting" option in RISKMAN. For the

scenario of increased female and male mortality, vulnerability was set at 0 for dependent bears, 0.42 for independent females, and 0.58 for independent males. This simulated higher protective status for females, and produced additional mortality ratios similar to the observed ratio of females to males in the annual estimates of total mortalities of independent bears (Table 4.4.1) and in the historical ratio of female to male mortalities during periods of legal hunting (Section 5). We started with 19 additional mortalities, because our calculated mortality thresholds suggested these would have been sustainable under the scenario of increased female and male mortality assuming an initial population size of 765 bears (Table 4.11.2). For the scenario of increased male mortality only, vulnerability was set at 0 for dependent bears and independent females and was set at 1 for independent males. Thus, all additional mortalities were drawn from independent males. We started with 24 additional male mortalities, because our calculated mortality thresholds suggested these would have been sustainable under the scenario of increased male-only mortality assuming an initial population size of 765 bears (Table 4.11.2). For both scenarios, we incrementally increased or decreased the number of additional mortalities from this starting number until we identified the highest number consistent with stability or growth. All simulations started with a stable age distribution based on observed vital rates. Given that this method effectively decreased the input independent survival rates as a function of the initial population size, Method 1 was particularly useful for evaluating the initial population estimate of 765 bears.

For Method 2, we utilized the series of models with varying rates of independent female and male survival from Section 4.10, and extrapolated the number of annual mortalities consistent with the varying independent survival rates from our estimated total annual mortality during 2004–2014, based on the ratio of the modeled to observed mortality rates of independent bears. For the scenario of increased female and male mortality, we started with a ratio of 1.60. In other words, if our observed independent mortality rates were consistent with a mean of 31 total annual mortalities of independent bears during 2004–2014, then mortality rates increased by 1.60 (i.e., 0.915 for females, 0.830 for males) should be consistent with a mean of 49 total annual mortalities (i.e., close to our calculated mortality threshold of 50, Table 4.11.2). For the scenario of increased male mortality only, we started with a ratio of 2.38, which was consistent with our calculated mortality threshold of 41 males (Table 4.11.2). For both scenarios, we incrementally increased or decreased the ratio from the starting point until we identified the highest number of total mortalities consistent with stability or growth. All simulations started with a stable age distribution based on observed vital rates. Given that this method was dependent on sustainable survival rates, which were relatively consistent across a range of population sizes, Method 2 was particularly useful for evaluating our annual counts of total mortality.

Results

Using Method 1, we estimated that 19 (8 female, 11 male) additional annual independent mortalities, above our observed count, would have been consistent with population decline during 2004–2014, under the scenario of increased female and male mortality (Table 4.11.3). Decreasing this number of additional mortalities, population stability was first observed when 13 (5 female, 8 male) additional mortalities were simulated, consistent with sustainable annual mortality of 44 independent bears (19 female, 25 male). This sustainable number of annual independent bear mortalities was approximately 88% of the calculated threshold (Table 4.11.2).

Under the scenario of increased male mortality only, we found that 24 additional annual independent male mortalities during 2004–2014 would have been consistent with population decline according to Method 1 (Table 4.11.4). Decreasing this number of additional male mortalities, population stability was first observed when 18 additional male mortalities were simulated, consistent with sustainable annual mortality of 49 independent bears (14 female, 35 male). This sustainable number of annual independent bear mortalities was approximately 84% of the calculated mortality threshold (Table 4.11.2).

Using Method 2, survival rates associated with an extrapolated annual count of 49 total independent mortalities (22 female, 27 male) would have been consistent with population decline during 2004–2014, under the scenario of increased female and male mortality (Table 4.11.5). Decreasing the modeled-to-observed mortality ratio, population stability was first observed with a ratio of 1.32, consistent with an extrapolated annual count of 41 total independent mortalities (18 female, 23 male). This extrapolated number of sustainable annual independent bear mortalities was about 82% of the calculated mortality threshold (Table 4.11.2).

Under the scenario of increased male-only mortality, an extrapolated annual count of 50 total mortalities (14 female, 40 male) would have been consistent with population decline during 2004–2014 (Table 4.11.6). Decreasing the modeled-to-observed mortality ratio, population stability was first observed with a ratio of 1.90, consistent with an extrapolated annual count of 46 total mortalities (14 female, 32 male). This extrapolated number of sustainable annual independent bear mortalities was about 79% of the calculated mortality threshold (Table 4.11.2).

Using the two different methods, with different underlying assumptions, we obtained estimates of sustainable mortality that were relatively similar (Table 4.11.2), however both methods indicated our calculated mortality thresholds likely would have been too high if they had been applied during 2004–

2014. In other words, had our mean estimate of total independent bear mortality met this threshold, population decline likely would have resulted. If we assume our vital rates were relatively accurate, the discrepancy between the sustainable mortality and the calculated mortality thresholds could either be explained by overestimation of the population size in 2004 and/or underestimation of the total annual mortality of independent bears. Among the various data sets used in our analyses, the records of reported versus unreported mortalities among our radio-marked sample was the most limited, therefore perhaps the most likely explanation for the discrepancy may be an underestimation of the Bayesian inflation factor used to estimate unreported mortality. To account for either of these potential underestimations, we multiplied the calculated mortality thresholds by 80% (Table 4.11.2) to produce adjusted mortality thresholds, as a function of estimated population size (Table 4.11.7).

Applying the mortality thresholds for the management scenario of increased female and male mortality to our annual median modeled population size during 2004–2014, we find that total estimated annual mortality numbers for both females and males fell below thresholds during 9 of 11 years (82%) and exceeded thresholds during 2 of 11 years (18%). Considering total mortality thresholds (females and males combined), estimated annual mortality numbers fell below thresholds during all years (Figure 4.11.1). Similarly, applying mortality thresholds relative to the lower 95th percentile of modeled population size during 2004–2014, we find that total estimated annual mortality numbers for both females and males fell below thresholds during 9 of 11 years (82%) and exceeded thresholds during 2 of 11 years (18%). Considering total mortality thresholds (females and males combined), estimated annual mortality numbers fell below thresholds 8 of 11 years (73%) and slightly above thresholds during 3 of 11 years (27%). Given the wide variability in estimated annual mortality (partially due to the Bayesian inflation method), occasional years of mortality exceeding the threshold is still consistent with positive growth during the period.

Applying the mortality thresholds for the management scenario of increased male mortality only to our annual median modeled population size during 2004–2014, we find that total estimated annual mortality numbers for females fell below thresholds during 6 of 11 years (55%) and exceeded thresholds during 4 of 11 years (45%). Mortality numbers for males or combined sexes fell below all thresholds (Figure 4.11.2). Results were similar applying mortality thresholds to the lower 95th percentile of modeled population size during 2004–2014. Given that this management scenario involved a decrease in male survival, but no change in independent female survival, it is expected that female mortality thresholds would be exceeded during approximately half of the years.

To project mortality thresholds into the future, assuming no change in vital rates or trajectory, we would estimate a total median population size of 982 bears in 2015, corresponding with a mortality threshold of 52 independent bears (22 females, 30 males) under the management scenario of increased female and male mortality, and a mortality threshold of 59 independent bears (17 females, 42 males) under the management scenario of increased male-only mortality. Alternately, these mortality thresholds might be applied to the lower 95th percentile of the population estimate (i.e., 851 bears), resulting in a mortality threshold of 46 independent bears (20 females, 26 males) under the management scenario of increased female and male mortality, and a mortality threshold of 52 independent bears (15 females, 37 males) under the management scenario of increased male-only mortality. If we assume no temporal trend in estimated total mortality during 2004–2015, the mean projected estimate of total mortality would be 31 total bears in 2015. Conversely, if we assume a slight increasing trend in total estimated mortality during 2004–2015, the mean projected estimate of total mortality would be 36 bears in 2015. Both projected numbers fall below these estimated mortality thresholds, indicating that approximately 10–28 additional mortalities would likely be sustainable, depending on the management scenario (mixed-sex or male only) and the population estimate (median or lower 95th percentile) selected.

Table 4.11.2. Calculated sustainable mortality thresholds for the NCDE grizzly bear population within the DMA for 2004 based on an estimated population size of 765 bears (Kendall et al. 2009); and results of two evaluations of these thresholds based on stochastic population modeling and comparisons with total estimated mortality during 2004–2014. Two management scenarios were modeled: increased mortality of independent (≥2 years old) females and males and increased mortality of independent males only.

Management scenario	Sex	Mean estimated total mortality 2004–2014[a] (A)	Calculated mortality thresholds (Population size = 765)		Sustainable mortalities (Method 1)			Sustainable mortalities (Method 2)		
			Threshold[b] (B)	Additional (B - A)	Additional[c] (C)	Total (A + C)	Proportion of threshold ([A + C] / B)	Total[d] (D)	Additional (D - A)	Proportion of threshold (D / B)
Female and male	Female	14	22	8	5	19	0.86	18	4	0.82
	Male	17	28	11	8	25	0.89	23	6	0.82
	Total	31	50	19	13	44	0.88	41	10	0.82
Male only	Female	14	17	3	0	14	0.82	14	0	0.82
	Male	17	41	24	18	35	0.85	32	15	0.78
	Total	31	58	27	18	49	0.84	46	15	0.79

[a] Mean annual estimates of total number of independent female and male mortalities during 2004–2014, using Bayesian methods (Table 4.4.4).

[b] Calculated annual mortality thresholds based on an estimated population size of 765 bears in 2004 (Table 4.11.1).

[c] Maximum number of additional annual mortalities (above total estimated mortality [A]) that would have been sustainable during 2004–2014, as estimated using the "hunting" option in RISKMAN (with a sex-selective ratio of 0.58 M:0.42 F), a starting population size of 765, and observed recruitment and survival rates (Tables 4.11.3 and 4.11.4).

[d] Maximum number of annual mortalities that would have been sustainable during 2004–2014, as estimated by multiplying the observed number of annual mortalities (A) by the ratio of the lowest sustainable mortality rate to the observed mortality rate (Tables 4.11.5 and 4.11.6).

Table 4.11.3. Method 1 evaluation of calculated sustainable mortality thresholds for grizzly bears in the NCDE during 2004–2014 under a management scenario of additional female and male mortality. Model results were obtained from stochastic population modeling with RISKMAN software, based on observed vital rates (recruitment; and dependent and independent [≥2 years old] bear survival), and 2000 simulations/model. Additional annual mortalities of independent bears were entered using the "hunting" option, which effectively decreased the input independent survival rates as a function of the initial population size entered as 765 (Kendall et al. 2009). Parameters consistent with population growth or stability were: mean population growth rate of ≥1.00; probability of decline ≤0.10; and median population size ≥ initial population size. Shaded values signify when criteria were consistent with declining population trajectory.

	Values entered into models					Output from models							
	Independent survival		Mean additional annual mortalities of independent bears[b]			Geometric mean growth rate		Probability of decline[c]		Final N (median, 10 yrs)	Final N (lower 95th percentile, 10 yrs)	Mean age (10 yrs)	
Initial N[a]	Female	Male	Total	Female	Male	5 yrs	10 yrs	5 yrs	10 yrs			Female	Male
765	0.947	0.895	10	4.2	5.8	1.009	1.009	0.05	0.04	845	723	7.7	4.9
765	0.947	0.895	11	4.6	6.4	1.008	1.008	0.06	0.06	833	717	7.7	4.9
765	0.947	0.895	12	5.0	6.9	1.007	1.007	0.07	0.07	822	704	7.7	4.8
765	0.947	0.895	13	5.4	7.5	1.006	1.006	0.09	0.09	812	693	7.7	4.8
765	0.947	0.895	14	5.9	8.1	1.004	1.004	0.12	0.14	798	678	7.6	4.7
765	0.947	0.895	15	6.3	8.6	1.003	1.002	0.16	0.17	787	676	7.6	4.7
765	0.947	0.895	16	6.7	9.2	1.002	1.001	0.17	0.21	782	662	7.6	4.6
765	0.947	0.895	17	7.1	9.8	1.000	1.000	0.22	0.30	765	646	7.6	4.6
765	0.947	0.895	18	7.5	10.3	0.998	0.998	0.23	0.34	756	642	7.6	4.5
765	0.947	0.895	19	7.9	10.9	0.997	0.997	0.28	0.42	747	626	7.6	4.4

[a] Population size.

[b] Additional annual mortalities were input as a total for both sexes with a sex selective ratio of 0.58 M:0.42 F, thus the total number and sex-specific numbers varied stochastically among runs.

[c] Decline defined as final N <95% of initial N.

Table 4.11.4. Method 1 evaluation of calculated sustainable mortality thresholds for grizzly bears in the NCDE during 2004–2014 under a management scenario of additional male mortality only. Model results were obtained from stochastic population modeling with RISKMAN software, based on observed vital rates (recruitment; and dependent and independent [≥2 years old] bear survival), and 2000 simulations/model. Additional annual mortalities of independent males were entered using the "hunting" option, which effectively decreased the input independent survival rates as a function of the initial population size entered as 765 (Kendall et al. 2009). Parameters consistent with population growth or stability were: mean population growth rate of ≥1.00; probability of decline ≤0.10; and median population size ≥ initial population size. Shaded values signify when criteria were consistent with declining population trajectory.

	Values entered into models					Output from models							
	Independent survival		Mean additional annual mortalities of independent bears[b]			Geometric mean growth rate		Probability of decline[c]		Final N (median, 10 yrs)	Final N (lower 95th percentile, 10 yrs)	Mean age (10 yrs)	
Initial N[a]	Female	Male	Total	Female	Male	5 yrs	10 yrs	5 yrs	10 yrs			Female	Male
765	0.947	0.895	15	0	15.0	1.006	1.008	0.05	0.01	866	742	7.8	3.7
765	0.947	0.895	16	0	16.0	1.006	1.008	0.06	0.01	860	737	7.8	3.6
765	0.947	0.895	17	0	17.0	1.004	1.007	0.07	0.02	853	733	7.8	3.5
765	0.947	0.895	18	0	17.9	1.003	1.005	0.09	0.02	845	727	7.8	3.4
765	0.947	0.895	19	0	18.9	1.002	1.005	0.11	0.03	842	721	7.8	3.2
765	0.947	0.895	20	0	19.9	1.001	1.004	0.12	0.04	835	712	7.8	3.1
765	0.947	0.895	21	0	20.9	0.999	1.002	0.15	0.05	825	708	7.8	3.0
765	0.947	0.895	22	0	21.9	0.998	1.002	0.16	0.06	823	703	7.8	2.9
765	0.947	0.895	23	0	22.9	0.997	1.000	0.19	0.08	818	698	7.8	2.7
765	0.947	0.895	24	0	23.9	0.995	0.999	0.22	0.09	811	682	7.8	2.6

[a] Population size.

[b] Additional annual mortalities were input as a total for males only.

[c] Decline defined as final N <95% of initial N.

Table 4.11.5. Method 2 evaluation of calculated sustainable mortality thresholds for grizzly bears in the NCDE during 2004–2014 under a management scenario of additional female and male mortality. Model results were obtained from stochastic population modeling with RISKMAN software, based on some observed vital rates (recruitment; cub and yearling survival), but varying rates of independent (≥2 years old) female and male survival. The number of annual mortalities consistent with the varying independent survival rates were extrapolated from the mean estimated total mortality observed, based on the ratio of model to observed rates of independent mortality. Parameters consistent with population growth or stability were: mean population growth rate of ≥1.00; probability of decline ≤0.10; and median population size ≥ initial population size. Shaded values signify when criteria were consistent with declining population trajectory.

Values entered into models			Output from models								Extrapolation of total mortality			
	Independent survival		Geometric mean growth rate		Probability of decline[b]		Final N (median, 10 yrs)	Final N (lower 95th percentile, 10 yrs)	Mean age (10 yrs)			Extrapolated total mortality		
Initial N[a]	Female	Male	5 yrs	10 yrs	5 yrs	10 yrs			Female	Male	Ratio[c]	Female	Male	Total
765	0.945	0.890	1.023	1.020	<0.01	<0.01	938	815	7.8	5.3	1.04	14	18	32
765	0.940	0.880	1.015	1.015	0.01	<0.01	887	775	7.8	5.2	1.13	16	19	35
765	0.935	0.870	1.009	1.009	0.04	0.02	843	732	7.7	5.0	1.23	17	21	38
765	0.930	0.860	1.004	1.004	0.10	0.09	800	692	7.7	4.9	1.32	18	23	40
765	0.925	0.850	0.998	0.998	0.23	0.27	758	655	7.7	4.7	1.42	20	24	44
765	0.920	0.840	0.992	0.993	0.37	0.51	725	613	7.6	4.6	1.51	21	26	47
765	0.915	0.830	0.986	0.987	0.60	0.79	685	584	7.6	4.5	1.60	22	27	49

[a] Population size

[b] Decline defined as final N <95% of initial N.

[c] Ratios of modeled to observed mortality rates, which were applied to mean estimated annual total mortality during 2004–2014 (13.8 F, 16.9 M) to extrapolate numbers of annual mortalities consistent with modeled mortality rates.

Table 4.11.6. Method 2 evaluation of calculated sustainable mortality thresholds for grizzly bears in the NCDE during 2004–2014 under a management scenario of additional male mortality only. Model results were obtained from stochastic population modeling with RISKMAN software, based on some observed vital rates (recruitment; cub and yearling survival), but varying rates of independent (≥2 years old) female and male survival. The number of annual mortalities consistent with the varying independent survival rates were extrapolated from the mean estimated total mortality observed, based on the ratio of model to observed rates of independent mortality. Parameters consistent with population growth or stability were: mean population growth rate of ≥1.00; probability of decline ≤0.10; and median population size ≥ initial population size. Shaded values signify when criteria were consistent with declining population trajectory.

Values entered into models			Output from models									Extrapolation of total mortality			
	Independent survival		Geometric mean growth rate		Probability of decline[b]		Final N (median, 5 yrs)	Final N (lower 95th percentile, 5 yrs)	Mean age (10 yrs)			Extrapolated total annual mortality			
Initial N[a]	Female	Male	5 yrs	10 yrs	5 yrs	10 yrs			Female	Male	Ratio[c]	Female	Male	Total
765	0.947	0.830	1.008	1.010	0.04	<0.01	805	719	7.8	3.9	1.62	14	27	41
765	0.947	0.820	1.007	1.010	0.04	0.01	803	717	7.8	3.7	1.71	14	29	43
765	0.947	0.810	1.004	1.007	0.07	0.01	794	708	7.8	3.5	1.81	14	31	45
765	0.947	0.800	1.002	1.006	0.08	0.01	788	701	7.8	3.4	1.90	14	32	46
765	0.947	0.790	1.000	1.004	0.11	0.02	782	697	7.8	3.2	2.00	14	34	48
765	0.947	0.780	0.998	1.003	0.15	0.03	776	690	7.8	3.1	2.10	14	35	49
765	0.947	0.770	0.997	1.002	0.16	0.02	773	688	7.8	2.9	2.19	14	37	51
765	0.947	0.760	0.994	1.000	0.18	0.04	767	680	7.8	2.8	2.29	14	39	53
765	0.947	0.750	0.991	0.998	0.23	0.04	758	647	7.8	2.7	2.38	14	40	54

[a] Population size

[b] Decline defined as final N <95% of initial N.

[c] Ratios of modeled to observed mortality rates, which were applied to mean estimated annual total mortality during 2004–2014 (13.8 F, 16.9 M) to extrapolate numbers of annual mortalities consistent with modeled mortality rates.

Table 4.11.7. Adjusted mortality thresholds, as a function of estimated population size, for independent (≥2 years old) grizzly bears in the NCDE under two management scenarios.

| Estimated population size (N) | Estimated mortality thresholds for independent bears[a] | | | | | |
| | Scenario of additional female and male mortality | | | Scenario of additional male mortality only | | |
	Female[b]	Male[c]	Total	Female[d]	Male[e]	Total
500	11	15	26	9	22	31
550	13	17	30	10	24	34
600	14	18	32	10	26	36
650	15	20	35	11	28	39
700	16	21	37	12	30	42
750	17	23	40	13	32	45
800	18	24	42	14	35	49
850	20	26	46	15	37	52
900	21	27	48	16	39	55
950	22	29	51	17	41	58
1000	23	30	53	17	43	60
1050	24	32	56	18	45	63
1100	25	33	58	19	48	67
1150	26	35	61	20	50	70
1200	28	36	64	21	52	73

[a] Thresholds were calculated, by sex, as proportion of independent bears in population × (1 – lowest sustainable survival rate) × N, and were adjusted to account for uncertainty in various estimates by multiplying by 0.80

[b] $0.41 \times 0.07 \times N \times 0.80$ or 2.30% of N

[c] $0.27 \times 0.14 \times N \times 0.80$ or 3.02% of N

[d] $0.41 \times 0.053 \times N \times 0.80$ or 1.74% of N

[e] $0.27 \times 0.20 \times N \times 0.80$ or 4.32% of N
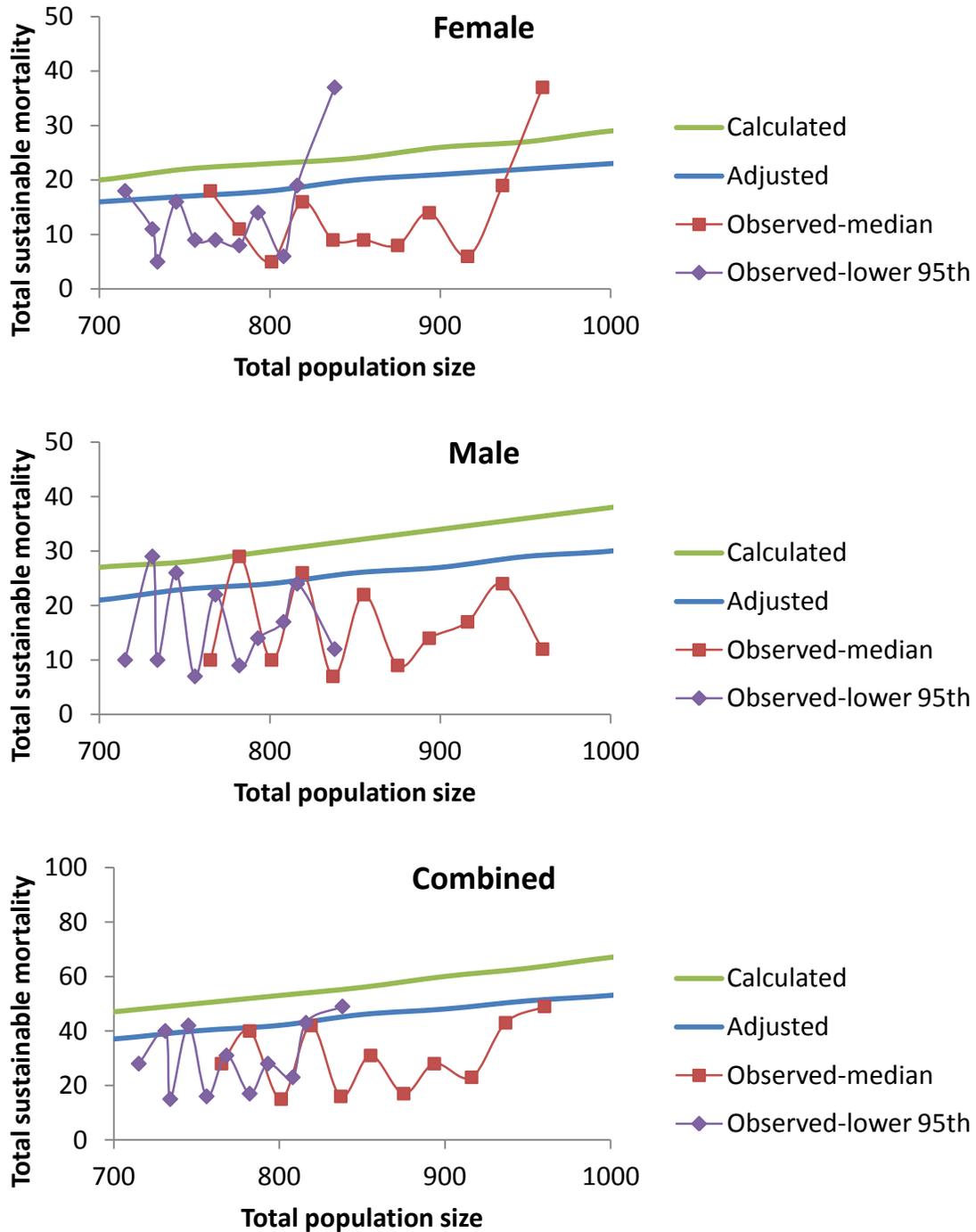
Figure 4.11.1. Estimated total number of mortalities of independent (≥2 years old) female (top), male (center), and combined (bottom) grizzly bears in the NCDE as a function of the median or lower 95th percentile of population size obtained from stochastic modeling for 2004–2014 (symbols), compared to calculated and adjusted mortality thresholds above which evidence of population decline was evident under the management scenario of increased mortality of independent females and males.
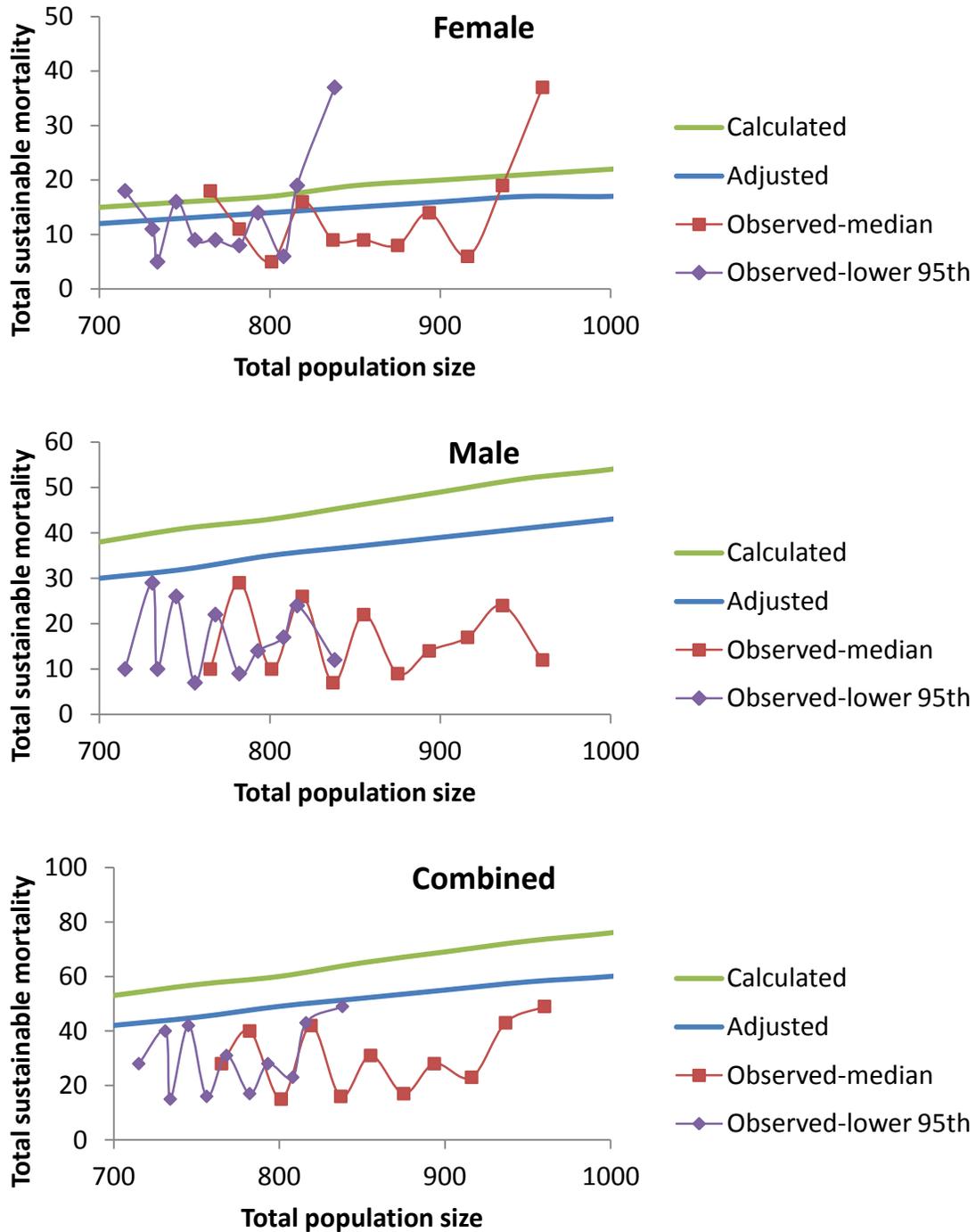
Figure 4.11.2. Estimated total number of mortalities of independent (≥2 years old) female (top), male (center), and combined (bottom) grizzly bears in the NCDE as a function of the median or lower 95th percentile of population size obtained from stochastic modeling for 2004–2014 (symbols), compared to calculated and adjusted mortality thresholds above which evidence of population decline was evident under the management scenario of increased mortality of independent males only.

5 DISCUSSION

When grizzly bears in the lower 48 states were listed as threatened under the Endangered Species Act in 1975, few reliable counts of population sizes were available, but populations were likely at very low densities, except perhaps for those centered in refugia like Glacier and Yellowstone National Parks. Hence, for the past 40 years, population growth and recovery has been our management goal, facilitated by efforts to minimize human-caused mortalities, especially for independent female bears. Various habitat management measures, especially those centered on National Forest lands, have also served to protect vital habitat and reduce human access and conflict, contributing to the productivity of bear populations and the reduction in human-caused mortality of bears. Within the NCDE and the GYE, these measures have resulted in population recovery. During the 1990s and the 2000s, evidence indicates both populations have grown, with some current estimates nearing 1000 bears for both ecosystems (IGBST 2013, this report). The NCDE population has essentially doubled its range. Previously confined primarily to the 23,000 km^2 PCA, the population has now expanded to inhabit over 53,000 km^2. Similar expansion of the GYE population has been documented (Bjornlie et al. 2014). Perhaps more than ever before, this range expansion, coupled with increasing human development, places grizzly bears and sizable human populations in close proximity in Montana. While suitable habitat exists for further expansion in some regions, grizzly bears are possibly reaching their biological and socially acceptable limits in others. Thus, the challenges of coexistence will occupy wildlife managers for years to come, and continued efforts by wildlife agencies, human communities, and land owners to reduce bear-human conflict will be vital.

The recovery of these populations also signals a paradigm shift in their management. Where robust population growth was once the management goal, more active population management accommodating a wider variety of stakeholders while maintaining healthy populations may be the management goal in the future. In the early days of ESA protection, nearly every reproductive female was considered essential to population recovery. Still today, removal of reproductive females is minimized. But, wildlife managers are increasingly eager for more flexibility in dealing with bear-human and bear-livestock conflicts, especially when individuals are involved in repeated conflict and when females are potentially passing on conflict behavior to their dependent offspring. The Draft Conservation Strategy (USFWS 2013) succinctly described the management challenge for the future:

> "The key to public support and successful management of grizzly bears is to balance multiple land uses, public safety, and careful consideration of grizzly bear needs. Human-caused mortality is the limiting factor for nearly all grizzly bear populations in the world and this Conservation Strategy aims to manage mortality at sustainable levels

through habitat protections that minimize mortality risk while emphasizing conflict prevention, conflict response, and decisions grounded in scientific data and monitoring. On both public and private lands, public information and education efforts have played, and will continue to play, an integral role in minimizing grizzly bear/human conflicts. Similarly, the responsive management of nuisance grizzly bears that increased public support and tolerance while grizzly bears have been listed as a "threatened" species under the ESA, will continue. In a recovered, delisted population of grizzly bears, management as game animals is a valuable conservation tool that can increase public support among those living in grizzly bear habitat. As such, management may include regulated hunting when and where appropriate."

Previous studies have shown that grizzly bear populations can sustain a certain level of mortality before populations decline (Bunnell and Tait 1981, Schwartz et al. 2003). Like other wildlife species, grizzly bears are subject to both natural and human-caused sources of mortality. Natural mortalities dominate among juvenile age classes, while many if not most adult mortalities are from human causes. Larger grizzly bear populations can often sustain some level of human-caused mortality above baseline levels, and sustainable rates therefore vary among areas depending on local demographic parameters (Bunnell and Tait 1981, Miller 1990, McLoughlin 2003). Coupled with previous studies, our results suggest that the NCDE grizzly bear population is numerically large relative to previous estimates (Dood et al. 1986, Dood and Pac 1993, Pac and Dood 1999, Kendall et al. 2009), demographically healthy, and still growing. As such, we have shown that some additional mortality would be sustainable. The current population monitoring program, involving capture and radio-telemetry studies to document vital rates, documentation and estimation of annual mortalities, and examination of the distribution of reproductive females and the total population provides data necessary to track changes in population parameters and trajectory.

This report provides the latest information obtained from these monitoring programs and utilized population modeling to estimate sustainable survival rates and to project sustainable numbers of mortalities for the near future. Population modeling provided information such as population growth rate, probability of population decline, and other information on age structure and population size, that can be used by managers to set mortality thresholds in the future. The stochastic modeling accounts for uncertainty of our vital rates and thus encapsulates many best-case and worst-case scenarios. Nonetheless, as shown in the population modeling section, the numbers of additional sustainable annual mortalities of independent bears are not large, and the difference between sustainable numbers and those that would be consistent with population decline are very close. Therefore, we must also caution managers that the consequence of error in population management is high as grizzly bears reproduce slowly and reduced populations will require many years to recover (Miller 1990).

Comparison between Findings of Mace et al. (2012) and this Report

The previous analysis of grizzly bear vital rates in the NCDE encompassed the years 2004–2009 and was restricted to those bears captured as part of the research sample (Mace et al. 2012). By including additional data from 2010–2014, as well as previously withheld data from bears captured in conflict and other situations, we were able to increase sample sizes substantially. The inclusion of management covariates was necessary to evaluate the potential effects of conflict behavior, management capture, and/or translocation on vital rates, but still allowed use of data from all monitored bears to obtain unbiased estimates for the population as a whole.

Our analyses presented in this report resulted in vital rate estimates that differed slightly from Mace et al. (2012; Table 5.1) and led to a slightly lower estimate of the annual rate of population growth ($\lambda = 1.023$) for the NCDE grizzly bear population than that previously reported ($\lambda = 1.031$; Mace et al. 2012). We do not believe the observed difference in the two estimates is a result of actual population change. Our current models included a covariate for trend, and no negative trend was observed in any of the vital rates. Rather, we believe that the differences between Mace et al. (2012) and this report can be attributed to: (1) an increase in sample sizes for estimation of all vital rates; (2) better representation of conflict females in the estimation of vital rates; and (3) subtle but significant differences in methods of analysis. For example, Mace et al. (2012) assumed that yearlings survived on the east side of the Continental Divide when separated from their mothers, whereas the current analysis assumed these yearlings died. Mace et al. (2012) estimated subadult and adult survival separately, whereas the current analysis combined all independent bears for a single survival rate. We also utilized covariates for analyses, while Mace et al. (2012) did not. The most substantial differences in vital rates were among those related to reproduction, namely cub and yearling survival, and the stable state proportion of females with cubs. Survival rate estimates for independent females were very similar between the two analyses. Finally, survival of independent males was not part of the analyses of Mace et al. (2012), but is included in our analyses.

Both the previous and current estimates of λ are consistent with positive population growth in the NCDE. Based on the previous estimate of 1.032 (Mace et al. 2012) and an initial population of 765 bears in 2004 (Kendall et al. 2009), population size estimates at 5 and 10 years would be 891 and 1,038. Based on our revised estimate of 1.023, population size estimates would be 857 and 960 at 5 and 10 years, respectively.

Table 5.1. Comparison of vital rates of grizzly bears in the NCDE from Mace et al. (2012) and this report.

Vital rate	Mace et al. 2012			This analysis		
	n	Estimate	95% CI	*n*	Estimate	95% CI
Independent female survival	181	0.923[a]	0.817–0.972	453	0.947[b]	0.913–0.969
Cub survival[c]	60	0.612	0.301–0.818	146	0.553	0.432–0.708
Yearling survival	34	0.682	0.258–0.898	109	0.639	0.502–0.816
Proportion of females with cubs	95[d]	0.322	0.262–0.382	232[d]	0.287	0.227–0.347
Litter size	30	2.27		110	2.10	
Age of primiparity[e]	10	5.4		31	5.7	
Population growth rate (λ)		1.031			1.023	

[a] Mace et al. (2012) estimated survival of subadults (0.851) and adults (0.952) separately; estimate is a sample-weighted mean for comparison.
[b] Mean of estimates with unknown fates censored versus assumed dead.
[c] Mace et al. (2012) assumed early independence for some yearlings; this study assumed all missing yearlings were mortalities.
[d] Sample size for reproductive transition analysis.
[e] This study utilized the Garshelis et al. (1998) unbiased estimator. Due to smaller sample size, Mace et al. (2012) did not use the unbiased estimator, therefore estimates in Mace et al. (2012) may be biased low.

Comparison between Findings and Draft Conservation Strategy

Using vital rates as estimated by Mace et al. (2012), Harris used Monte Carlo methods available in PopTools to conduct stochastic life-table analyses (Appendix 2C, Draft Conservation Strategy, USFWS 2013). He ran a series of simulations varying rates of independent female survival between 0.87 and 0.95, at increments of 0.01, to estimate what levels of survival were consistent with population stability, based on λ. Based on these analyses, the Draft Conservation Strategy put forth the following standards: (#2) Manage for survival of independent females generally > 0.90 in the PCA and Zone 1; and (#3) Independent female mortality will not exceed 10% of the estimated number of independent females. The Draft Conservation Strategy also proposed the following standard regarding male mortality: (#4) Independent male mortality will not exceed 20% of the estimated number of independent males.

Our current results, based on substantially more vital rate data from 2004-2014 and analyses involving both male and female bears, indicate that an independent female survival rate of 0.90 is likely not sustainable in the long term. We confirmed that an independent male survival rate of 0.80 is likely sustainable, but only as long as female survival rates are close to 0.95. Assuming observed recruitment rates, we found that median modeled population size declined by 16% at 5 years and 31% at 10 years when independent female survival was 0.90 and independent male survival was 0.80, regardless of initial population size (Section 4.11). Instead, our results suggested that independent female survival rates ≥0.930 are more appropriate for long-term persistence of the NCDE grizzly bear population, assuming

recruitment rates observed during 2004-2014 continue into the future (Figure 5.1). If additional mortality of females is anticipated, independent male survival rates ≥0.86 are more appropriate for long-term persistence of the NCDE grizzly bear population.

Presumably, standards #2 and #3 converted sustainable survival rates (e.g., 0.90 independent female survival) directly into thresholds for numbers of total estimated annual mortalities (e.g., 10% of estimated number of independent females). Standard #4 was also likely based on a sustainable survival rate of 0.80 for independent males. Our modeling, which incorporated both sustainable survival rates and observed numbers of estimated total annual mortalities, indicated this approach would likely overestimate sustainable mortality numbers. Given our current monitoring program, mortality thresholds of 6% for independent females and 11% for independent males are more appropriate for long-term persistence of the NCDE grizzly bear population.
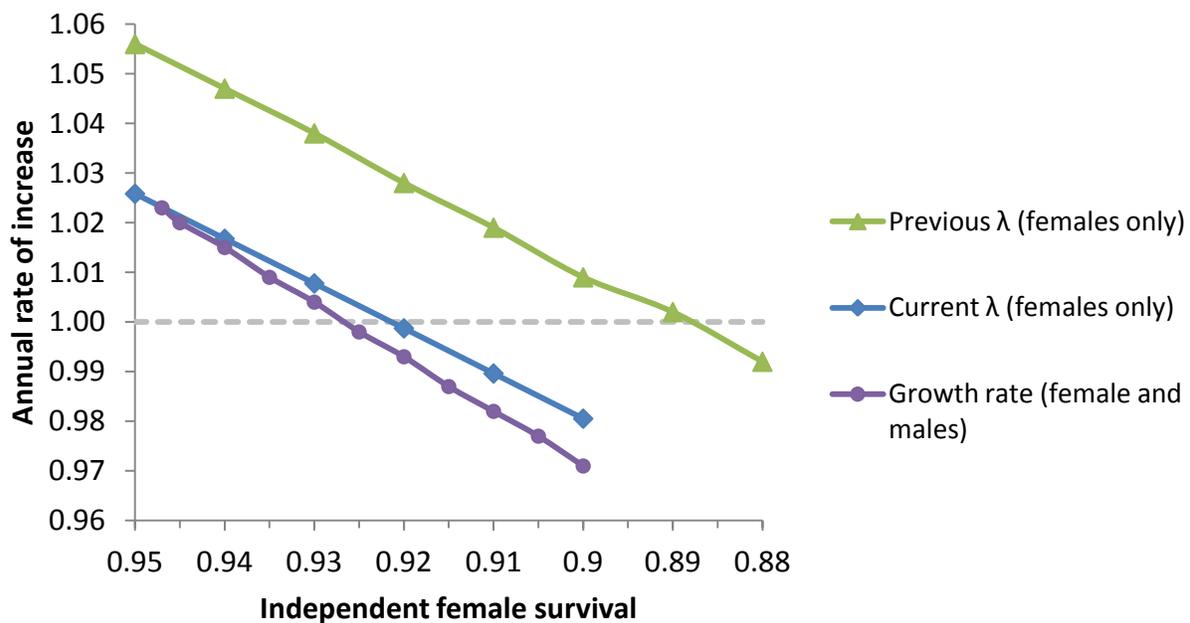
Figure 5.1. Comparison of sustainable independent (≥2 years old) female survival rates for grizzly bears in the NCDE between that reported in the Draft Conservation Strategy and this report. The previous intrinsic growth rate ([λ] based on recruitment and survival schedules of females only) was estimated using stochastic life table analyses (USFWS 2013, Appendix 2C), based on observed vital rates for 2004–2009. The current λ estimate was estimated using static life table analysis, based on observed vital rates for 2004–2014. The growth rate (based on recruitment and both female and male survival schedules) was estimated using RISKMAN stochastic modeling, based on observed vital rates for 2004–2014.

Influence of Conflict and Management on Vital Rates

Our results indicated that independent bear survival was negatively influenced by their recent conflict management history, with an effect lasting about 2 years in females and 4 years in males. Researchers observed a similar 2-year effect of management on grizzly bear survival in the GYE, when both sexes were combined (Haroldson et al. 2006). This result is not surprising given that human causes account for the majority of independent grizzly bear mortalities in the NCDE and management removal was a frequently observed cause of death among both females and males. Most management removals involve bears with habitual conflict behavior or bears that pose an immediate danger to humans. Still, our results demonstrate the effectiveness of efforts to mitigate conflict by MFWP and tribal personnel. Involvement in bear-human conflict is not synonymous with mortality, nor does it necessarily foretell future conflict activities. Time since last management capture was ≥5 years for 24% of research-captured bears with a management history, indicating that many bears involved in conflict are not chronic offenders and are capable of resuming natural foraging habits and human-accepted behaviors, especially if anthropogenic foods are secured. In a study of brown bear livestock depredation in Romania, Bereczky at al. (2011) estimated about 35% of damages were caused by repeat offenders exhibiting specialized predatory behaviors, while the remaining 65% were attributed to opportunistic predation. We found that within 2-4 years after a management capture, independent survival rates were indistinguishable from bears never captured in management situations.

Our covariate and model sets allowed us to distinguish translocation effects from management effects, and we found that translocation distance had a negligible-to-small, additive, negative effect on independent bear survival beyond the observed management effect. In our research sample, 76% of independent, management-captured bears were also translocated distances ranging from 8 to 215 km. The efficacy of translocation as a tool for solving bear-conflict problems is still debated; many authors cite frequent homing behavior and reduced post-transport survival as arguments against the use of translocation (Miller and Ballard 1982, Linnell et al. 1997, Campbell 1999, Fontúrbel and Simonetti 2011). Some even argue that translocation is equivalent to lethal control, because conflict bears are likely to die eventually anyway (Treves and Karanth 2003, Fontúrbel and Simonetti 2011). However, we found no translocation studies where researchers attempted to separate the effects of management capture (i.e., observed conflict behavior) and translocation. In the GYE, Blanchard and Knight (1995) reported lower survival for translocated grizzly bears than for bears that were not translocated, however the latter group included non-conflict bears captured for research. Consequently, similar to our results, their reported translocation effect may have been largely explained by the translocated bears' propensity for conflict behavior. Similarly, Comly-Gericke and Vaughan (1997) observed low survival rates for black bears

translocated ≥300 km in Virginia and argued that unfamiliar terrain and high mobility resulted in a high probability of encountering mortality sources, such as highways and roads. This argument was supported by the fact that automobile collisions were the major cause of mortality. However, lacking a survival comparison between translocated and non-translocated nuisance bears, these authors also failed to isolate the effects of translocation from the bears' propensity for nuisance behavior.

Our results indicating that survival was more affected by recent conflict behavior than translocation distance is further supported by the observed causes of death for those bears involved in management captures. When cause was determined, management removals and defense of property kills accounted for 61% of deaths, while vehicle or train collisions accounted for only 18%. In addition, only half of management-captured bears killed in collisions were translocated, indicating these deaths were not simply attributable to highly mobile translocated bears.

We did, however, find weak evidence for a possible translocation effect on cub survival, with lower survival within family groups translocated larger distances. Low survival rates for offspring translocated with their mothers were noted by Miller and Ballard (1982) for brown bear cubs and yearlings in Alaska and by Rogers (1986) for black bears cubs in various populations. Additional data are needed to determine if the translocation effect on cub survival is real for grizzly bears in the NCDE, however managers might consider the potential risk of long-distance translocation on cub survival. Nonetheless, the potential cost of translocation of young cubs is likely still less than the potential survival benefit of removing the mother from an active site of bear-human conflict if her continued presence in the area is likely to result in her removal. In the NCDE, Riley et al. (2004) evaluated the success of translocation of grizzly bears during 1975 to 1991. They estimated translocation was 44% successful, as defined by the cessation of conflict activities that required recapture within 2 years. Since that time, a number of additional efforts and programs have been implemented to reduce incidence of bear-human conflict, therefore a reevaluation of translocation success is warranted.

No management or translocation effects were apparent for other vital rates, indicating that pooling research and conflict bears for estimation of reproductive parameters does not introduce a bias. Several studies have reported that nuisance females were unlikely to produce cubs in the years following translocation (Miller and Ballard 1982, Brannon 1987, Comly-Gericke and Vaughan 1997), but this effect was not detected in our reproductive transition analysis.

Setting Sustainable Mortality Thresholds

Our modeling results provided valuable data for establishing sustainable survival rates and/or mortality thresholds for independent bears for the near future (e.g., 1–5 years), assuming continuation of observed rates of recruitment and dependent bear survival. As described in Section 4.11, we found that independent female survival rates ≥ 0.93 were most likely to lead to population stability or growth. Independent male survival rates ≥ 0.86 were most associated with sustainability and sex ratios and age structures similar to those presently observed. Independent male survival rates between 0.80 and 0.85 were sustainable, as long as female survival rates were near 0.950, however these rates resulted in more skewed female-to-male sex ratios and a decreased representation of adult males in the population. Relating these sustainable survival rates to data on estimated total mortality during 2004–2014, estimated sustainable mortality thresholds, as a function of estimated population size, were described in Table 4.11.7.

Continued monitoring of grizzly bear survival rates (cub, yearling, independent female, and independent male) and reproductive parameters (annual proportion of independent females with cubs, mean litter size) will be needed to periodically reevaluate application of these estimates of sustainable survival and sustainable mortality numbers for independent females and males. Specifically, model sets for estimating grizzly bear vital rates should continue to include covariate(s) for assessing whether rates change over time, with special attention on any negative trend. For the period 2004–2014, our models included a linear time trend, but as more years are added to analyses, it will be possible to utilize more complex temporal covariates, such as quadratic or sigmoidal functions. For example, researchers tested models with 8 different temporal covariates to assess changes in grizzly bear vital rates in the GYE for a 29-year time series spanning 1983–2012 (van Manen et al. 2015). This type of analysis would be particularly important for: (1) detecting changes in recruitment and dependent bear survival that might require adjustment of sustainable mortality thresholds for independent females and males; and (2) detecting changes in independent survival rates associated with management decisions to allow for additional mortalities through increased management removals or legal hunting.

Any observed temporal changes in grizzly bear vital rates (as described above) should be incorporated into future population modeling to assess recent and long-term trends in grizzly bear population growth and trajectory. For the period 2004–2014, when no temporal changes in vital rates were detected, we used single estimates for each of the recruitment and survival parameters, but again, as more years are added to analyses, more complex models will likely be necessary to account for detected temporal changes in vital rates or to account for management decisions to allow for additional mortalities through increased management removals or legal hunting.

As previously observed, the estimated numbers of additional annual mortalities differed between the mixed-sex and male-only management scenarios. Thus, besides selecting an overall population size goal, managers need to select a management program. For example, a mixed-sex mortality program with females accounting for 40-45% of the additional annual mortality, would allow for additional removals of bears of both sexes involved in conflict situations, and would be consistent with observed sex ratios typically achieved through hunting (Miller et al. 2003, Kojola et al. 2003) and previously observed in Montana when hunting was permitted (Table 5.2, Figure 5.2). Alternatively, a male-only mortality program, which skews additional annual mortalities toward males, while maintaining female mortalities at low levels, would allow for additional removals of males captured in conflict situations. Such a management program would skew the population sex-age structure toward females and younger males, which should also be considered.
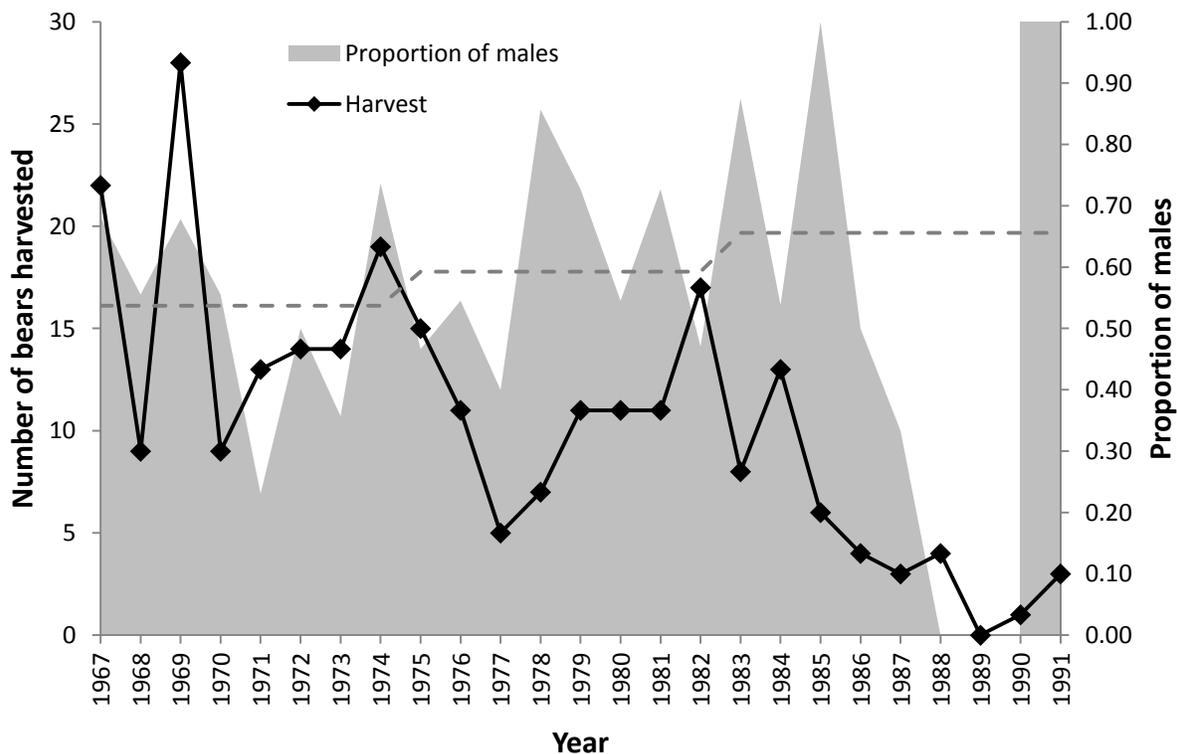

Figure. 5.2. Number of grizzly bears harvested (black line) and proportion of males in kill (gray area), NCDE, 1967–1991. Mean proportion of males (gray dashed line) differed slightly with changes in regulations: 1967–1974 (no quota); 1975–1982 (combined-sex quota for human-caused mortalities); and 1983–1991 (combined-sex quotas and female sub-quotas for human-caused mortalities).

Even in the absence of human-caused mortality, males typically have lower survival rates than females in bear populations, especially among subadult age classes (Schwartz et al. 2003). Subadult males are far more likely to engage in natal dispersal (Mace and Waller 1998, McLellan and Hovey 2001, Zedrosser et al. 2007), a behavior that often incurs survival costs in solitary carnivores (Waser et al. 1994). Thus, it is not unusual for females to outnumber males in bear populations. In essence, mortality thresholds that favor females not only serve to protect the reproductive segment of the population, but also reflect relatively natural conditions. However, management decisions to maximize survival rates of females, while reducing survival of males, will increase the magnitude of the skew in sex ratio and the sex differences in age structure. While a highly skewed sex-age structure is likely not preferred for the population at large, the active manipulation of sex-age structure on a local scale may help alleviate some bear-human conflict issues.

Table 5.2. Timeline of changes to grizzly bear hunting regulations in Montana.

Year	Management event or regulation change
1923	Bears declared game animals.
	Any person with a general big game license permitted to harvest a grizzly bear within described seasons and areas.
1942	Spring grizzly bear hunting season closed statewide.
1947	Harvest of cubs or females with cubs prohibited.
1948	Baiting of bears prohibited.
1967	*Grizzly bear listed as endangered under the Endangered Species Preservation Act.*
	Grizzly bear mortality records maintained in one location.
	Special grizzly bear license is required to hunt grizzly bears and may be obtained at any time before or during the season.
	The cost of the license is $1 for residents and $25 for non-residents, with additional purchase of a $25 trophy license required within 10 days of harvesting a grizzly bear.
	Harvest limit of one grizzly bear/person/license year established.
1969	Mandatory reporting of grizzly bear kills implemented with presentation of hide and head.
1970	Last date of grizzly bear license purchase set at September 15 (the day prior to the first general big game hunting season).
1971	Increase in grizzly bear license fees to $5 residents and $35 for non-residents. The $25 trophy license remains.
	Waiting period of 7 years established for next purchase of a grizzly bear license by successful grizzly bear hunters.

Year	Management event or regulation change
1972	Last date of grizzly bear license purchase set at July 1.
	Baiting with livestock, trapping devices, and pursuit with dogs are all prohibited as methods of legal harvest of grizzly bears.
1975	*Grizzly bear listed as a threatened species in the lower 48 states*
	10 hunting districts established in the NCDE. Hunting closed in other areas of the state.
	Annual quota of 25 human-caused deaths of grizzly bears established (including hunting) for the NCDE.
1976	Increase in grizzly bear license fees to $25 for residents and $125 for non-residents.
	Regulation enacted that the grizzly bear hunting season closes within 48 hours of notice when the number of bears killed by humans reaches 25.
1978	Last date of license purchase set at June 15.
1980	Increase in grizzly bear license fee to $150 for non-residents.
1982	Increase in grizzly bear license fee to $175 for non-residents.
	Last date of grizzly bear license purchase set at August 31.
1983	Annual sub-quota of 9 human-caused deaths of female grizzly bears established (including hunting) for the NCDE.
1984	Increase in grizzly bear license fees to $50 for residents and $300 for non-residents.
1985	USFWS issues emergency rule to allow grizzly bear hunting along the Rocky Mountain Front and to adjust quotas.
1986	Annual quota of human-caused grizzly bear deaths adjusted to 21 bears and annual sub-quota adjusted to 6 females in the NCDE.
	Three bear management units established in the NCDE with additional female sub-quotas in each.
1987	State law passed limiting harvest to one grizzly bear/person/lifetime.
1991	A limited entry, spring grizzly bear hunting season implemented on the Rocky Mountain Front.
	Fall grizzly bear hunting season cancelled due to a federal court preliminary injunction on all hunting of grizzly bears.
1992	Grizzly bear hunting season omitted from biennial regulations for 1992–1993.
	Authority for state to establish grizzly bear hunting season in the NCDE removed under federal rule.

6 PROPOSED MONITORING AND REPORTING PROTOCOLS

Monitoring Area

Grizzly bear population monitoring, population objectives, and mortality management for the NCDE should occur within the DMA. To ensure that the radio-marked sample is representative of this core region of the NCDE and corresponds to estimates of total mortality obtained within the DMA:

1. Research captures for the trend monitoring sample should be confined to the DMA.
2. Efforts to distribute the sample throughout the DMA subunits, roughly in proportion to estimated relative grizzly bear density should continue.
3. Data, especially those obtained from bears captured for management purposes, should be screened to exclude bears principally residing outside of the DMA.

Mortality Reporting

1. Grizzly bear mortality records should be maintained for all known and probable deaths within and adjacent to the DMA.
2. All known and probable mortalities should be categorized by sex and age class (COY, yearling, subadult [2-4 years], and adult [≥5 years old]), when known. For reporting purposes, when sex of a dead bear is unknown, it should be randomly assigned as female or male. Similarly, when age class of a dead bear is unknown, it should be randomly assigned as dependent versus independent. These assignments will be maintained as part of the long-term reported mortality record, with notation that they were randomly assigned.
3. An annual tally should be kept of known and probable mortalities of independent females and males within the DMA, by sex, using the following discovery classifications (defined in Table 4.4.1):
   a. The number of management removals of independent-aged bears (including capture mortalities and bears removed and translocated out of the NCDE);
   b. The number of deaths of independent-aged bears wearing functional radio-transmitters (excluding management removals);
   c. The number of deaths of other independent-aged bears reported or discovered/reported to management agencies.
4. The number of reported and unreported independent bear deaths occurring annually should be estimated as a function of reported deaths using the procedure of Cherry et al. (2002) and as modified in this document (i.e., with high and low reporting categories). The sample of radio-marked females and males used to estimate reporting rate for the Bayesian analysis should be pooled, unless sample

sizes increase sufficiently to conduct separate analyses for each sex. However, the reporting rate estimates and Bayesian inflation factors should be applied separately to each sex. We suggest that the estimates of reporting rates be updated every 5 years as additional data become available from radio-marked bear deaths.

5. Estimated total number of mortalities of independent female and male bears should be calculated as the sum of management removals, radio-collared deaths, and reported and unreported deaths.

6. For independent bears, documented and estimated total mortality should be reported annually. For dependent young, documented mortality should be reported annually.

Distribution of Reproductive Females

Bear Management Units (BMUs) should be used to assess the distribution of reproductive females within the PCA. A reproductive female is an individual accompanied by cubs, yearlings, or 2-year-old offspring. An annual tally is maintained of reproductive females within each BMU using verified visual/photographic observations, known or probable mortalities, DNA detections, or observations of radio-marked family units. Per the demographic standard in the Recovery Plan (1993) and Draft Conservation Strategy (USFWS 2013), the presence of reproductive females is to be documented in 21 of 23 BMUs at least once every 6 years. We suggest a starting year of 2004. In addition, occupancy of supplementary BMUs within Zone 1 should be monitored and reported.

Population Distribution

The geographic distribution data of female and male grizzly bears should be updated periodically (i.e., every 1–5 years) using: location data from radio-marked bears; capture and mortality locations; grizzly bear-human conflict sites; observations (sighting or track) that were confirmed by agency personnel; and other biological samples (hair, blood, scat, or tissue) that have been confirmed through DNA analysis to belong to the NCDE population. To ensure consistency over time, verified observations should be placed on a 7 km^2 grid over the area using GIS, and the extent of bear distribution should be estimated using the method of Bjornlie et al. (2014).

General Approach to Estimating Vital Rates, Population Trend, and Population Size

1. We recommend a radio-marked sample of at least 25 research females and 5–10 research males be maintained annually within the DMA. Vital rate information should also be collected on all radio-marked conflict males and females. In the event that additional discretionary mortalities are sanctioned in the final Conservation Strategy, we recommend radio-monitoring of additional males and females outside of Glacier National Park to more accurately assess the impact of additional

mortality on annual survival rates. The necessary sample size and study duration should be determined by simulation modeling and power analyses.

2. The estimation of population vital rates and trend, based on the sample of radio-marked grizzly bears, should be based on the methods outlined in this report and that of Mace et al. (2012), unless more applicable techniques are recommended. To minimize uncertainty associated with survival estimates, every effort should be made to verify the fate of bears whose radio transmitter pulse-rate indicates a possible mortality.

3. The estimate of population size for a given year should be the median estimate obtained using stochastic population modeling involving observed time-specific rates of recruitment, dependent bear survival, and female and male independent bear survival, with an initial population size based on Kendall et al. (2009). Over time, efforts should be made to obtain independent estimates of population size to calibrate our modeled estimates.

General Approach to Managing Mortality

1. The long-term population objective for the NCDE and the DMA should follow those set forth in the final NCDE Grizzly Bear Conservation Strategy.

2. Annual mortality thresholds should be established for independent (≥2 years old) female and male bears, based on demographic criteria set forth in the final NCDE Grizzly Bear Conservation Strategy and using guidance set forth in this document.

3. Given that most mortality of cubs and yearlings (68%) was likely not from human causes during our study period, and most dependent young mortalities likely occur without our detection (except for those of radio-marked females), we do not recommend establishing mortality thresholds for dependent young.

4. Based on ongoing monitoring of vital rates, the Population Monitoring Team should provide periodic estimates of population trend and population size (e.g., every 5 years), and continue to evaluate the effects of total annual mortality on the NCDE population. Managers and decision-making bodies can then use these estimates to set mortality thresholds for a specified time frame within the DMA to achieve objectives set forth in the final NCDE Grizzly Bear Conservation Strategy.

5. If the population objectives and standards in the final NCDE Grizzly Bear Conservation Strategy allow, additional discretionary mortality for each sex could be allocated to additional removals of bears involved bear-human conflict and/or state- or Tribal-sanctioned hunting.

6. Conflict bear management control guidelines should be set forth in the finalized NCDE Grizzly Bear Conservation Strategy.
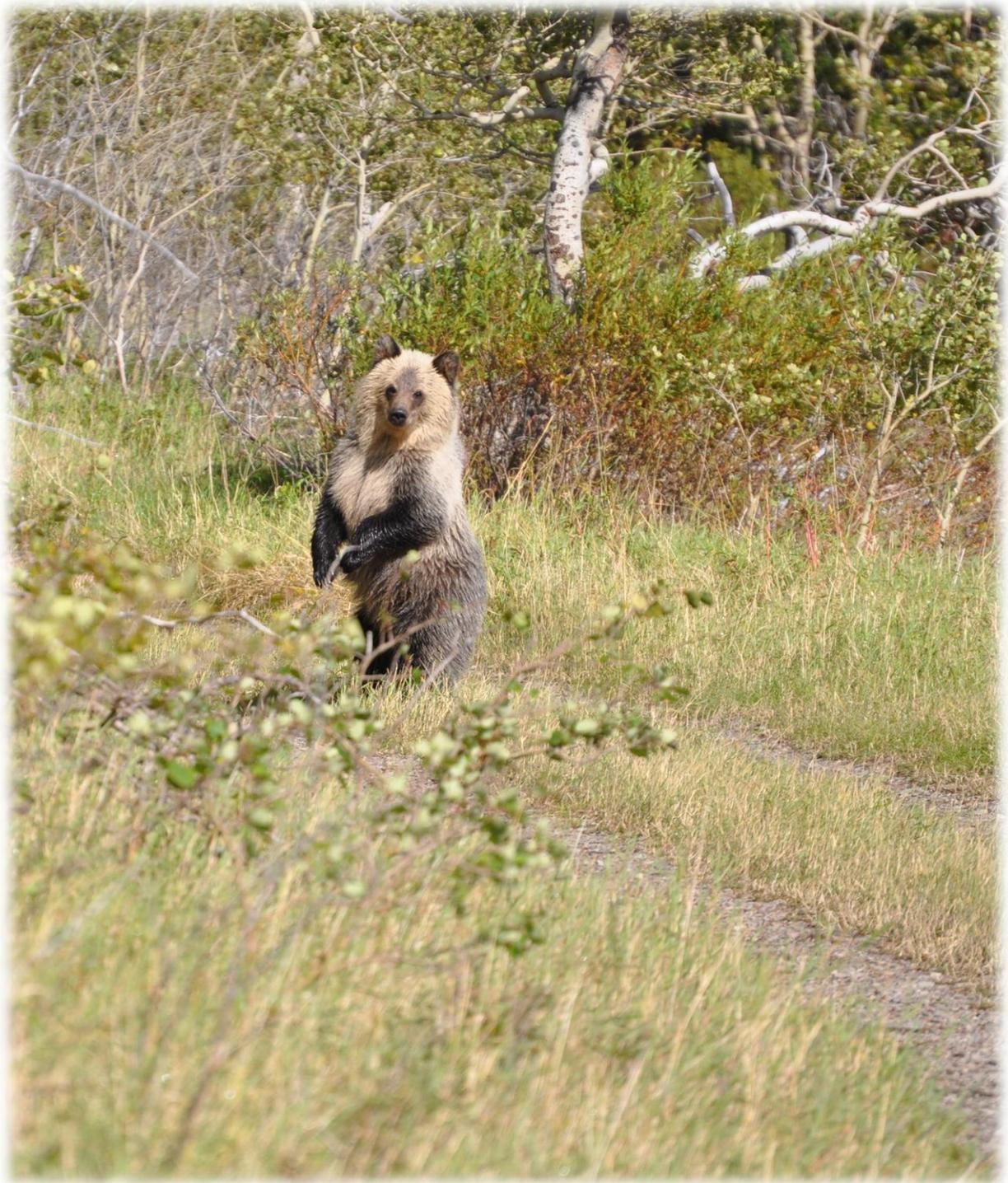
7 LITERATURE CITED

Aune K and W Kasworm. 1989. Final report: east front grizzly studies. Montana Department of Fish, Wildlife and Parks, Helena.

Bereczky L, M Pop, and S Chiriac. Trouble-making brown bear *Ursus arctos* Linnaeus, 1758 (Mammalia: Carnivora) – behavioral pattern analysis of the specialized individuals. Travaux du Muséum National d'Histoire Naturelle 54:541–554.

Bishop CJ, G White, and PM Lukacs. 2008. Evaluating dependence among mule deer siblings in fetal and neonatal survival analyses. Journal of Wildlife Management 72:1085–1093.

Bjornlie DD, DJ Thompson, M Haroldson, CC Schwartz, K Gunther, S Cain, DB Tyers, K Frey, and BC Aber. 2014. Methods to estimate distribution and range extent of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Society Bulletin 38: 182–187.

Blanchard BM and RR Knight. 1995. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. Journal Wildlife Management 59: 560–565.

Brannon RD. 1987. Nuisance grizzly bear, Ursus arctos, translocations in the Greater Yellowstone Area. Canadian Field Naturalist 101:569–575.

Brannon RD, R Mace, and A Dood. 1988. Grizzly bear mortality in the Northern Continental Divide Ecosystem, Montana. Wildlife Society Bulletin 16:262–269.

Bunnell FL and DEN Tait. 1981. Population dynamics of bears – implications. Pp. 75–98 *in* CW Fowler and TD Smith, eds. Dynamics of Large Mammal Populations. John Wiley and Sons, New York.

Campbell BH. 1999. Homing of translocated brown bears (*Ursus arctos*) in coastal south-central Alaska. Northwestern Naturalist 80:22–25.

Cherry S, MA Haroldson, J Robinson-Cox, and CC Schwartz. 2002. Estimating total human-caused mortality from reported mortality using data from radio-instrumented grizzly bears. Ursus 13:175–184.

Comly-Gericke LM and MR Vaughan. 1997. Survival and reproduction of translocated Virginia black bears. Ursus 9:113–117.

Cooch E and G White (eds). 2014. Program MARK: a gentle introduction. Available online at http://www.phidot.org/software/mark/docs/book.

Craighead J, J Sumner, and G Scaggs. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlife-Wildlands Institute Monograph 1. University of Montana, Missoula.

Dinsmore SJ, GC White and FL Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83:3476–3488.

Dood A, SJ Atkinson, and VJ Boccadori. 2006. Grizzly bear management plan for western Montana: final programmatic environmental impact statement 2006–2016. Montana Department of Fish, Wildlife and Parks, Helena.

Dood AR, RD Brannon, and RD Mace. 1986. The grizzly bear in northwestern Montana: final programmatic environmental impact statement. Montana Department of Fish, Wildlife and Parks, Helena, Montana.

Dood AR and HI Pac. 1993. The grizzly bear in northwestern Montana: five year update of the programmatic environmental impact statement 1986–1990. Montana Department of Fish, Wildlife and Parks, Helena.

Eberhardt LL and RR Knight. 1996. How many grizzlies in Yellowstone? Journal of Wildlife Management 60:416–421.

Efron B and G Gong. 1983. A leisurely look at the bootstrap, jackknife, and cross-validation. American Statistician 37:36–48.

Esler D, DM Mulcahy, and RL Jarvis. 2000. Testing assumptions for unbiased estimation of survival of radiomarked harlequin ducks. Journal of Wildlife Management 64:591–598.

Fontúrbel FE and JA Simonetti. 2011. Translocations and human-carnivore conflicts: problem solving or problem creating? Wildlife Biology 17:217–224.

Garshelis DL, K Noyce, and PL Coy. 1998. Calculating average age of first reproduction free of the biases prevalent in bear studies. Ursus 10:437–447.

Haroldson MA, CC Schwartz, and GC White. 2006. Survival of independent grizzly bears in the Greater Yellowstone Ecosystem, 1983–2001. Pages 33–42 *in* Schwartz, CC, MA Haroldson, GC White, RB Harris, S Cherry, KA Keating, D Moody, and C Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 61.

Heisey DM and TK Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management. 49:668–674.

Interagency Grizzly Bear Study Team. 2007. Summary and explanation of methods to estimate population size and sustainable mortality of Yellowstone grizzly bears. Interagency Grizzly Bear Study Team, U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana.

Interagency Grizzly Bear Study Team. 2012. Updating and evaluating approaches to estimate population size and sustainable mortality limits for grizzly bears in the Greater Yellowstone Ecosystem. Interagency Grizzly Bear Study Team, U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana.

Kendall KC, JB Stetz, J Boulanger, AC McLeod, D Paetkau, and GC White. 2009. Demography and genetic structure of a recovering grizzly bear population. Journal of Wildlife Management 73:3–16.

Kendall KC, JB Stetz, DA Roon, LP Waits, J Boulanger, and D Paetkau. 2008. Grizzly bear density in Glacier National Park, Montana. Journal of Wildlife Management 70:1693–1705.

Knight RR, BM Blanchard, and LL Eberhardt. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. Wildlife Society Bulletin 23:245–248.

Kojola I, PI Danilov, H Laitala, V Belkin, and A Yakimov. 2003. Brown bear population structure in core and periphery; analysis of hunting statistics from Russian Karelia and Finland. Ursus 14:17–20.

Linnell JDC, R Aanes, JE Swenson, J Odden, and ME Smith. 1997. Translocation of carnivores as a method for managing problem animals: a review. Biodiversity and Conservation 6:1245–1257.

Mace RD, DW Carney, T Chilton-Radandt, SA Courville, MA Haroldson, RB Harris, J Jonkel, B McLellan, M Madel, TL Manley, CC Schwartz, C Servheen, G Stenhouse, JS Waller, and E Wenum. 2012. Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. Journal of Wildlife Management 76:119–128.

Mace RD, TL Manley, and KE Aune. 1994. Factors affecting the photographic detection rate of grizzly bears in the Swan Mountains, Montana. International Conference on Bear Research and Management 9:245–251

Mace RD and JS Waller. 1998. Demography and population trend of grizzly bears in the Swan Mountains, Montana. Conservation Biology. 12:1005–1016.

McLellan BN and FW Hovey. 2001. Natal dispersal of grizzly bears. Canadian Journal of Zoology 79:838–844.

McLellan B, F Hovey, R Mace, J Woods, D Carney, M Gibeau, W Wakkinen, W. Kasworm. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management: 63: 911–920.

McLoughlin PD. 2003. Managing risks of decline for hunted populations of grizzly bears given uncertainty in population parameters. Final Report to British Columbia Independent Scientific Panel on Grizzly Bears. Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

Miller SD. 1990. Population management of bears in North America. International Conference on Bear Research and Management 8:357–373.

Miller SD and WB Ballard. 1982. Homing of transplanted Alaskan brown bears. Journal of Wildlife Management. 46:869–876.

Miller SD, RA Sellers, and JA Keay. 2003. Effects of hunting on brown bear cub survival and litter size on Alaska. Ursus 14:130–152.

Montana Department of Fish, Wildlife and Parks. 2004. Biomedical protocol for free-ranging Ursidae in Montana: black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos horribilis*): capture, anesthesia, surgery, tagging, sampling and necropsy procedures. Montana Department of Fish, Wildlife and Parks, Helena.

Pac HI and AR Dood. 1999. The grizzly bear in northwestern Montana: five year update of the programmatic environmental impact statement 1991–1995. Montana Department of Fish, Wildlife and Parks, Helena.

Pollock KH, SR Winterstein, CM Bunck, and PD Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Riley SJ, K Aune, RD Mace, and MJ Madel. 2004. Translocation of nuisance grizzly bears in northwestern Montana. Ursus 9:567–573.

Rogers LL. 1986. Effects of translocation distance on frequency of return by adult black bears. Wildlife Society Bulletin 14:76–80.

Schwartz CC and GC White. 2008. Estimating reproductive rates for female bears: proportions versus transition probabilitites. Ursus 19:1–12.

Schwartz CC, MA Haroldson, and S Cherry. 2006. Reproductive performance of grizzly bears in the Greater Yellowstone Ecosystem, 1983–2002. Pages 18–23 *in* CC Schwartz, MA Haroldson, GC White, RB Harris, S Cherry, D Moody, and C Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of the Yellowstone grizzly bear. Wildlife Monographs 161.

Schwartz CC, SD Miller, and MA Haroldson. 2003. Grizzly bear. Pages 556–586 in GA Feldhamer, BC Thompson, and JA Chapman, eds. Wild Mammals of North America: Biology, Management, and Conservation, second edition. Johns Hopkins University Press, Baltimore, MD, USA.

Stoneberg RP and CJ Jonkel. 1966. Age determination in black bears by cementum layers. Journal of Wildlife Management 30:411–414.

Taylor M, M Obbard, B Pond, M Kuc, and D Abraham. 2006. A guide to using RISKMAN: stochastic and deterministic population modeling risk management decision tool for harvested and unharvested populations. Department of Sustainable Development, Government of Nunavut, Iqaluit, Nunavut, Canada.

Treves A and KU Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:1491–1499.

U.S. Fish and Wildlife Service. 1993. Grizzly Bear Recovery Plan. U.S. Fish and Wildlife Service, Office of the Grizzly Bear Recovery Coordinator, University of Montana, Missoula.

U.S. Fish and Wildlife Service. 2013. Draft NCDE Grizzly Bear Conservation Strategy. U.S. Fish and Wildlife Service, Office of the Grizzly Bear Recovery Coordinator, University of Montana, Missoula. 127pp.

van Manen FT, MA Haroldson, DD Bjornlie, MR Ebinger, DJ Thompson, CM Costello, and GC White. 2015. Density dependence, whitebark pine, and vital rates of grizzly bears. Journal of Wildlife Management: DOI: 10.1002/jwmg.1005.

Waser PM, B Keane, SR Creel, LF Elliot, and DJ Minchella. 1994. Possible male coalitions in a solitary mongoose. Animal Behavior 47:289–294.

White GC and KP Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement. 120–138.

Wittinger WT. 2002. Grizzly bear distribution outside of recovery zones [digitized map]. USDA Forest Service, Northern Region Headquarters, Missoula, Montana, USA.

Woods JG, D Paetkau, D Lewis BN McLellan, M Proctor, and C Strobeck. 1999. Genetic tagging free ranging black and brown bears. Wildlife Society Bulletin. 27:616–627.

Zedrosser A, O Støen, S Sæbø, and JE Swenson. 2007. Should I stay or should I go? Natal dispersal in the brown bear. Animal Behavior 74:369–376.

8 APPENDICES

Appendix A. Analysis of potential bias when right-censoring undetected fates based on information obtained post monitoring

In known-fate monitoring, survival estimates assume that the probability of detection is independent of live or dead status (Cooch and White 2014). However, this assumption might be violated when a study animal's fate is undetected. Examples might include: (1) lost contact with a live animal due to premature transmitter failure; (2) lost contact with a live animal due to large movements outside of typical monitoring area and eventual transmitter expiration; (3) failure to retrieve a shed transmitter from a live animal to ascertain fate; (4) failure to retrieve a transmitter on a dead animal to ascertain fate; (5) lost contact with the transmitter of a live or dead animal due to obstruction; and (6) deliberate destruction of the transmitter on a dead animal to prevent discovery. The treatment of these cases of undetected fate is crucial for eliminating bias in estimates. One common approach to eliminate this bias is to run dual analyses: right-censoring animals with unknown fates to obtain a maximum survival rate and assuming death for these animals to obtain a minimum survival rate (Heisey and Fuller 1985, Pollock et al. 1989). We used this approach in our known-fate survival analysis for independent grizzly bears in the NCDE.

Although fates of are not always detected with telemetry, fate at last telemetry contact can be ascertained through observations occurring after the monitoring period, such as: (1) later live or DNA recapture; (2) later documented mortality; (3) later discovery of a shed collar through means other than telemetry; or (4) later discovery of a mortality or carcass through means other than telemetry. By revising the known-fate data with these discovered fates, it is possible to reduce the number of unknown fates (while maintaining the same number of telemetry months) and narrow the margin between the minimum and maximum survival rates. We used this approach in our analysis. Fates of 12 females and 25 males were undetected by telemetry, but 6 females and 16 males were verified to have been alive at the time of last telemetry contact through later live or DNA capture, later documented mortality, or later discovery of a shed collar. No monitoring-period mortalities were verified through later observation. By right-censoring these previously undetermined fates, we increased the minimum survival rate, but had no effect on the maximum survival rate. Six females and 9 males remained with truly unknown fates, and only these individuals were treated with the dual assignment of fate (right-censored and assumed dead).

An assumption of this approach is that survival rates of undetected animals are the same as detected animals (Esler et al. 2000). To test for a bias, we compared the proportions later observed (through recapture, mortality, or collar discovery) between bears with detected fates and bears with

undetected fates. Our unit of measure was a radio-transmitter deployment. We characterized each deployment by: year (at end of deployment), sex, fate (detected, undetected), and observed later (yes, no). We observed a decline in proportion observed later with year (as expected), therefore we ran a logistic regression with probability of later observation as the response; fate as a categorical predictor; and year as a covariate. Fate had no discernible effect on probability of later observation (Figure A1) for females (Wald$_1$ = 0.0, P = 0.99) or males (Wald$_1$ = 1.6, P = 0.20), suggesting our right-censoring of bears with discovered fates was random with respect to probability of survival.
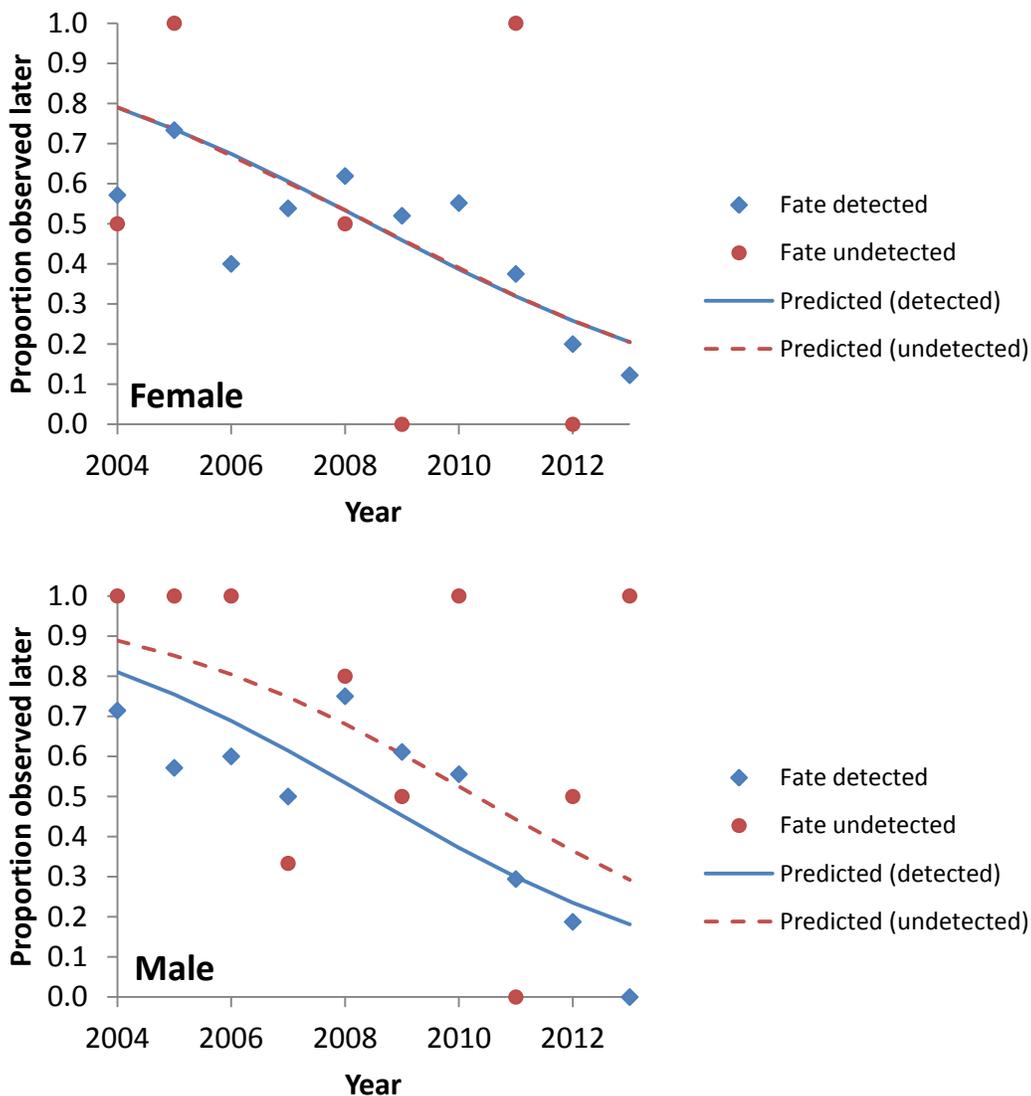

Figure A1. Observed and model-predicted proportions of radio-marked independent (≥2 years old) grizzly bears observed after the last radio-telemetry contact of a transmitter deployment (through recapture, mortality, or collar discovery), as a function of year and radio-telemetry detection of fate. Proportion observed later declined with year (P ≤ 0.001), but no difference was detected between bears with detected fates and bears with undetected fates (P ≥0.20).