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GRIZZLY BEAR POPULATION ECOLOGY AND MONITORING

DENALI NATIONAL PARK AND PRESERVE, ALASKA



Jeffrey A. Keay, Ph.D.

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Report of Project Development and Findings

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Jeffrey A. Keay, Ph.D.
Research Wildlife Biologist
Alaska Biological Science Center
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Jeffrey A. Keay, U. S. Geological Survey,
Alaska Biological Science Center, P.O. Box 9,
Denali Park, AK 99755 ^a

Abstract: The dynamics and ecology of a naturally regulated grizzly bear population were studied in Denali National Park and Preserve, Alaska, from 1991 through 1998. Bears were captured by helicopter darting and fitted with radio-transmitters containing mortality sensors. Bears were located at least monthly during the non-denning period. Density was determined by capture-mark-resight procedures. Serum antibody prevalence for infectious canine hepatitis, canine distemper, and leptospirosis were low indicating disease was not an important factor affecting population dynamics. Grizzly bear density, during fall 1995, was 27.1 independent bears/1000 km² (95% C.I. = 25.1 - 30.2) with 61% of the population marked. Adjusting survey area to reflect forage-producing habitat for more direct comparison with adjacent studies indicated 34.7 bears/1000 km² (95% C.I. = 32.2 to 38.7). Sight-ability of both females and males was high during the fall survey (60.7 % and 86.2%, respectively). The male age structure was unimodal, was 10% subadults, and included adults up to 16 years of age. The female age structure was strongly bimodal and 20% were subadults. The female segment experienced a shift in age distribution between 1991 and 1997; each

mode advanced 6 years but remained intact. There were 14% subadults in the 1991 female population and 3% in the 1997 population. Cubs-of-the-year experienced the lowest annual survival rates of all age classes at 0.341. Yearling survival was 0.455 and that of dependent 2-year-olds was 0.785. Subadult survival was 1.000 for females and 0.943 for males. Adult survival rates were 0.970 for females and 0.983 for males. Average age of first reproduction was 7.6 years and varied from 6 to 10. Litter size of cubs-of-the-year at the time of den emergence averaged 2.1. Dependent bears separated from their mothers at an average age of 2.9 years. Reproductive rates were 0.091 for 6-year-olds, 0.307 for bears 7 to 9 years old, 0.384 for bears 10 to 26, and 0.071 for bears 27 to 30 years of age. Bears averaged 23% to 27% body fat prior to den entrance in September. Females and subadult males had less than 10% body fat following den emergence in May. Adult males were 15% fat during May. Females lost 30% to 35% of total body mass and 18% to 20% of lean body mass during winter hibernation. High survival rates of independent bears and lack of human interference during the past 80 years suggests the Denali population is likely at carrying capacity. High dependent bear mortality coupled with periodic recruitment may allow the population to oscillate mildly but, in the long term, is likely stable. Implications for long-term monitoring are discussed.

^a Current address: U.S. Geological Survey, Eastern Regional Office, 1700 Leetown Road, Kearneysville, WV 25430

Grizzly bears (*Ursus arctos*) are an important ecological resource and an integral part of the naturally functioning predator-prey system of Denali National Park and Preserve, Alaska (Murie, 1981, Adams et al. 1995). Visitors also consider them an important part of their Denali experience, with 88% of the visitors that ride one of the bus services into the park observing grizzly bears in their natural habitat (Miller and Wright 1998). Human developments outside Denali National Park, proposed alternative access routes into the Park, and concerns regarding the impacts of human activities within the park resulted in the need for objective information regarding the status and trend of grizzly bears in Denali National Park and Preserve and for development of cost-effective, non-invasive methods to monitor the grizzly bear population.

The objectives of this paper are to 1) document the development and direction of grizzly bear research in Denali during the period 1991 to 1998, 2) present findings on grizzly bear population status and trend, and 3) describe efforts to develop noninvasive monitoring techniques.

STUDY OBJECTIVES

Study objectives varied during the 8 years of grizzly bear research in Denali. This work originated in 1991 as a small study to examine the role of grizzly bears as predators of caribou calves. Park staff redirected the study (August 1992) to develop non-invasive methods to monitor the grizzly bear population. Recent research (Samuel et al. 1987) had developed a technique for measuring visibility bias associated with aerial surveys that we felt could be applied in the open habitats of the Park. Consequently, during 1993 through 1995 our objectives were to 1) describe the characteristics of the existing population and 2) develop field methods for measuring visibility bias. Once developed, the non-invasive survey techniques would be

tested on the known population.

As opportunity permitted, we also began to collect data on factors that affected population dynamics in preparation for a second phase of broader, population ecology research. The objective was to identify factors that significantly affect grizzly bear population dynamics for possible inclusion in the Park's long term monitoring program. Unusually high grizzly bear cub mortality was noted early in the study. In 1994, we began measuring percent body fat using bioelectrical impedance analysis (Farley and Robbins 1994) to assess female physical condition. The goal was to see if cub mortality was related to female physical condition and, hence, nutritionally affected. We simultaneously initiated cooperative studies with Dr. Roseann Densmore and Dave Douglas, both of the Alaska Biological Science Center, to measure the abundance of important berry foods for bears and to assess the potential of Advanced Very High Resolution Radiometry (AVHRR) satellite data to predict berry abundance through correlation with plant phenology, biomass abundance, and standard weather parameters. Those studies will be reported separately by Densmore and Douglas.

By the end of 1995 we had good estimates of population density and sex and age structure. However, our final efforts to develop field methods to measure visibility bias were unsatisfactory. Dr. Pham X. Quang (mathematician, University of Alaska, Fairbanks) recommended using a binomial estimator that as yet was untested and not previously reported in the biological literature. In 1996, we altered objective 2) to conduct repeated aerial surveys, on the known density population, to obtain point and variance estimates to test the precision of the binomial estimator. Inclement weather precluded obtaining those data. Since we had completed a portion of objective 1) we also

altered capture objectives to focus on females to better measure cub production and survival. Collars were maintained on all previously radioed males and females to improve measures of survival for all age classes. However, we did not attempt to replace males whose transmitters were removed prematurely.

In late 1996 Park staff requested that we postpone final efforts to develop techniques to enumerate bears and begin more aggressively studying nutritional ecology. A study plan was developed in 1997 in cooperation with Dr. Charles Robbins, Washington State University, to address the new objectives. That study plan was rejected by the Park. Consequently, during 1997 we continued to 1) improve measures of reproductive and survival rates, and 2) assess female physical condition, using bioelectrical impedance analysis, to see if it could serve as a useful tool in elucidating the role of nutrition in rates of cub production and survival. Objectives during 1998 were limited to monitoring cub production and survival.

STUDY AREA

The McKinley Slope Study Area encompassed 1,750 km² along the north slope of the central Alaska Range in Denali National Park and Preserve, Alaska (formerly Mount McKinley National Park, Fig 1). The climate is generally cool and wet during the summer with temperatures typically 10 C to 15 C. Freezing temperatures and snow may occur during any month. Snow accumulation usually begins in October and dissipates from lowlands and unshaded portions of foothills by mid-May.

The area was delineated to include all important foraging habitats, including large, concentrated, berry patches on glacial moraines. Elevations ranged from 600 m to 2,000 m; high elevations above the vegetation line (>1500 m) were included as part of the study area because bears often denned there.

The study area included the principal calving grounds of the Denali Caribou Herd (*Rangifer terandus*, Adams et al. 1995). The

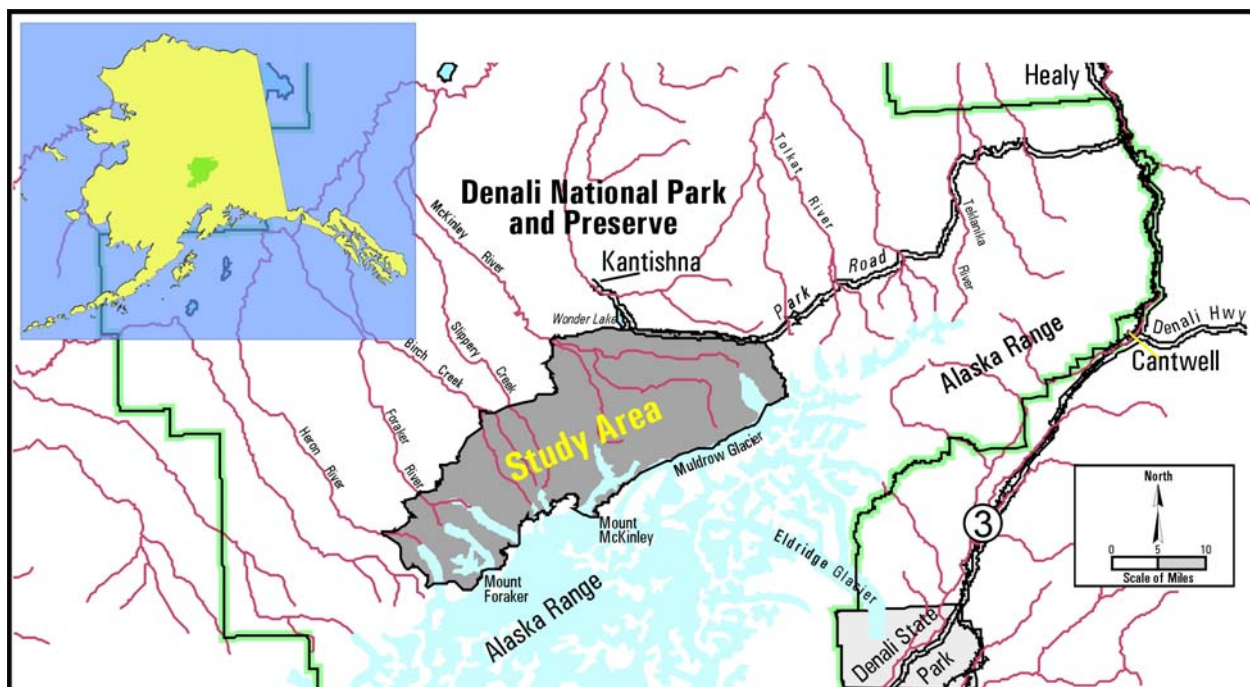


Figure 1. McKinley Slope grizzly bear study area, Denali National Park and Preserve, Alaska, 1991 through 1998.

Herd exceeded 20,000 animals in the early 1940's (Murie 1944), declined to around 5,000 by 1968, and varied from 1,000 to 3,000 during the period 1970 to 1998 (Haber 1977, Adams et al. 1989, Layne G. Adams, USGS, Biological Resources Division, Alaska Biol. Sci. Center, pers. commun.). Moose (*Alces alces*) densities in the study area were low and averaged 60 per 1000 km², below 1050m, during March 1992 (L. G. Adams, unpubl. data.).

There are no records or other indications of bear poaching within the study area. Meat hunting and trapping, which may have included limited bear harvest, did occur prior to establishment of the Park in 1917. Park-wide, back-country visitor use increased from 2,200 user-nights in 1971, to 10,000 in 1978. It averaged 11,400 from 1979 through 1990, and 15,500 during 1991-97. Within the study area, back-country use averaged 2,204 user-nights per year during this study. Most visitor use (63%) was concentrated on the eastern 15% of the study area (east of the Muldrow Glacier and north of the McKinley River). Overnight visitor densities averaged 8.2/1000 km² during the study but varied from 0.2 to 43.4 for various back-country units. Grizzly bears in the study area obtained human foods in no more than 10 reported human encounters in the past 18 years. There have been no management kills or translocations of nuisance bears to or from the study area. Consequently, human activities have had virtually no impact on grizzly bear population dynamics in the study area for at least 80 years.

METHODS

Population Ecology

Grizzly bears were captured by helicopter darting (Taylor et al. 1989). All captured bears were fitted with radio transmitters containing mortality sensors. Captures occurred annually during May 1991 through 1998, and September 1993 through 1997. Dependent bears were radio-collared at 2 years of age. We deter-

mined the ages of captured bears by counting cementum annuli (Matson et al. 1993) from a vestigial first premolar. The premolar was extracted at each bear's first capture to minimize age-related bias (Keay 1995). Age assignments were made by Matson's Laboratories, Milltown, Montana but were adjusted in 1 case when the body size of a dependent bear indicated otherwise (Keay 1995). Bears were classified as adults if ≥ 6 and subadults (reproductively immature) when independent but ≤ 5 years old.

During 1991-93, bears were located weekly from fixed-wing aircraft from the time of den emergence until den entrance; during 1994-98, weekly locations were limited to den emergence through June and September until den entrance. Cub production was determined by the number of young observed with a female at the time of den emergence. Cubs-of-the-year (COY) and yearlings were assumed dead if radio-marked females were later observed with smaller litters.

Survival of radio-collared bears was calculated with a modified Kaplan-Meier method (Pollock et al. 1989). Equation 2 (Pollock et al. 1989) was used to calculate variance because it is less sensitive to animals added or censored. Survival estimates for the 8-year study were converted to the parameter of interest, annual survival, by taking the 8th root of the point and interval estimates (Amstrup and Durner 1995). Bears were censored when transmitters were removed or stopped functioning. The finite rate of increase, or growth multiplier, was calculated using the Lotka equation (Caughley 1974:110). Age of first reproduction was calculated following procedures outlined by Garshelis et al. (1998). Reproductive rates (females produced per reproductive female) were calculated as one half of the number of cubs-of-the-year observed at den emergence divided by the number of adult females monitored.

Habitat availability was determined by

examining 199 randomly selected points in the study area on 31 August 1994. The study area boundary was digitized at a scale of 1 inch per mile and entered into an ArcInfo database. A digitized 1:250,000 elevation model, interpolated from 200 foot contours to meters, with 80 m horizontal and 1 meter vertical resolution (interpolated), was used to identify the 915 m (3,000 feet) contour. Horizontal spacing among candidate sample points was set at 100 m. Random points were selected by ArcInfo from each strata, above or below 915 m elevation, in proportion to the area of that strata (51% above 915 m and 49% below or equal to 915 m elevation). Each random point was located using a commercial global positioning system (GPS) mounted in a Piper supercub airplane. Vegetation type (Vierek et al. 1992, level 3) was recorded for a projected 30 m radius around the random point. (If candidate sample points were too far apart, some ground locations would have no probability of being sampled. If candidate sample points were too close together, then over-lapping radii of sample units would give some ground locations a higher likelihood of being sampled than others. Error associated with locating a random point on the ground using commercial global positioning systems effectively increases the sample unit radius with regards to its influence on the probability of sampling a specific ground location. To insure that all ground locations had an equal probability of being sampled, the horizontal spacing between random points was based on a combination of sample unit size plus anticipated random GPS error.)

Serum was extracted from blood samples collected during normal capture operations and stored at -10 C. Sera were analyzed at the Washington Animal Disease Diagnostic Laboratory (WADDL) for prevalence of infectious canine hepatitis, leptospirosis, and canine distemper. Dr. James Everman (DVM at WADDL) provided professional guidance and

directed the processing of samples. The standard threshold titer of 1:5 was considered evidence of previous exposure and referred to hereafter as “positive.” All lower titers were referred to as “negative.”

Brown bear density was determined from capture-mark-resight techniques (Miller et al. 1997) on a 1,707 ha portion of the study area during September 1995. Half of the study area was surveyed each day for six days providing 3 replicates. Density was calculated using maximum likelihood estimation (White 1996). An adjusted density based on forage producing habitat was estimated by subtracting the area of extensive, unvegetated habitats above 1,500 m (267 ha) and extensive glaciers and barren river bars (106 ha) that were surveyed during the density estimate. Bears were captured for 4 years prior to conducting the density estimate to assure a representative sample of all sex, age, and reproductive classes.

Sex and age structure were determined by the number of radio-collared bears detected within the study area while conducting capture-mark-resight density estimates (Miller et al. 1997). Sex and age data were weighted by the number of times each bear was in the study area during independent surveys conducted on different days, in order to minimize the bias of over-emphasizing animals with large home ranges. Female age structure in Denali during 1991 and 1997 was determined by the number of marked females known to be alive during those years; comparable data for males was not available.

Analysis of variance and t-tests were used to identify differences in body fat and weight between sex, age, and reproductive classes of bears ($\alpha = 0.05$).

Population Monitoring

Aerial Surveys. The use of radio collars to enumerate bears has become an established practice because 1) bear densities are low, 2) certain estimation procedures become available

when a known proportion of a population is observed, and 3) to at least partially compensate for differences in habitat use patterns of various sex, age, and reproductive classes of bears both within and between surveys, which affects the likelihood of their detection. Aerial surveys without the use of radio transmitters on bears would have to provide some adjustment for the visibility bias associated with differences in habitat use patterns of bears. Increasing survey intensity was used to measure visibility bias for moose when there was complete snow cover (Gasaway et al. 1986) but would not have adequate success for bears on snow-free ground. Double sampling has been used for sheep and is being tested for bears but will likely only work in high density populations (E. Becker, Alaska Dept. Fish and Game, pers. comm.).

Visibility bias associated with group size, behavior, and habitat, was successfully measured for elk using a second aircraft to monitor radioed animals that were missed by the survey aircraft and to determine the sighting conditions associated with missed observations (Samuel et al. 1987). Comparing sighting characteristics for animals missed to those for animals seen provided a means to estimate the proportion of animals observed under differing sighting conditions. Those proportions were then used to adjust results of aerial surveys. This procedure is widely used for elk in northern Idaho. Measuring visibility bias appeared to be the most plausible technique for bear populations at the low density and in the open habitats of Denali National Park. Three approaches were tested for measuring visibility bias which varied the way in which monitoring aircraft determined sighting conditions for animals missed during survey flights. Monitor aircraft 1) followed survey aircraft, 2) preceded and followed survey aircraft, and 3) conducted simultaneous observation through high altitude surveillance. Method development occurred in conjunction with radio-tracking or density

estimation efforts during May 1993 and September 1994 and 1995.

The ability of biologists and pilots to properly classify bears by sex and age category was tested during the 1995 density estimate. Survey aircraft were not informed of the sex, age, or reproductive status of marked bears. They were asked to record the radio frequency of marked bears and their best estimate of the bears sex, age, age class, and the number and age of dependent young, which were then compared to known values.

Thermal Infrared Imaging. Thermal infrared videography showed promise for aerial surveys of white-tailed deer (Wiggers and Beckerman 1993) and was investigated as a potential population monitoring technique for bears. Preliminary surveys of grizzly bears outside the Park, with thermal infrared videography, provided inconsistent results and left many questions regarding the potential usefulness of the technique (Miller and McDonald 1996). A study proposal was developed with Dr. Ernie Wiggers, University of Missouri, to elucidate problems encountered in those previous efforts and provide a more scientifically rigorous test of the technique than was conducted by Miller and McDonald (1996). Thermal infrared temperatures were obtained from sedated bears and their surrounding environment using an Omega OS85-EM infrared thermometer (Omega engineering, Inc., Stanford, CT 06907). This thermometer measures surface temperature in the 8-14 micron wavelength, similar to aerial infrared scanners. Bear surface temperatures were measured at six locations with the thermometer held 50 cm from and perpendicular to the surface of interest: forehead, spine between shoulders, spine at approximately 10 cm above base of tail, side at mid-ribcage, one foreleg just above the elbow, and one hind leg just above the knee. At each temperature location the degree of moisture (dry, moist, wet), and

whether the measurement was taken in high, direct sunlight, low-angle sunlight, or shade was recorded. Coat color and rectal temperature were recorded. Guard hair length was measured along the spine between the shoulders as an indicator of the amount of insulation between the skin and measured surface of the bear. Background temperature (vegetation, soil, etc.) was measured at each of the 4 cardinal points 4 m away from the bear's position. The vegetation type (Vierek et al. 1992, level 3), whether it was in sunlight or shade, and its phenology was recorded. Time of day, ambient air temperature, cloud cover, and precipitation condition were recorded for each bear measured.

RESULTS

Population Ecology

Habitat Availability. Low shrub habitats were the predominant vegetation types and occurred on 31.7% of the study area (Table 1). Tall shrubs occupied 14%, herbaceous 16.1%, and forest habitats covered 12.1% of the study area. Sites devoid of vegetation occurred at

26.1% of the random points visited and were primarily above 1,500 m. The most abundant terrain features were flat terrain and gentle slopes (< 30 degrees) at 33.7% and 24.1%, respectively (Table 2). Steep slopes (30 – 60 degrees) and rolling terrain each occupied 16.6% of the study area. River bars occurred on 9% of the random sites visited.

Disease. Serum antibody prevalence of infectious canine hepatitis was 6% ($n = 17$) for adult females (positive titer 1:5) and 0% ($n = 5$) for cubs-of-the-year captured in September 1994. Prevalence was 17% ($n = 12$) for sera collected from adult females during May, 1991 and 1992 (positive titers 1:10 and 1:40). One female tested positive in both 1992 and 1994. Six females that tested negative in 1991-92 were also negative in 1994. Prevalence of canine distemper was 8% ($n = 12$) for adult females in 1991-92 (positive titer 1:10). There was no evidence of exposure to leptospirosis for adult females in 1991 and 1992 ($n = 12$).

Density. Grizzly bear density was 27.1 independent bears/1000 km² (95% C.I. = 25.1 -

Table 1. Percentage of each vegetation classification (Vierek et al. 1992, level 3) observed at random points within the McKinley Slope grizzly bear study area, Denali National Park and Preserve, Alaska, August 1994.

Vegetation Class	> 3,000 ft.	≤ 3,000 ft	Combined	# Random Points
Forest, broadleaf, closed	0.0	2.1	1.0	2
Forest, conifer, closed	0.0	1.0	0.5	1
Forest, conifer, open	0.0	21.6	10.6	21
Scrub, low, closed	3.9	19.6	11.6	23
Scrub, low, open	13.7	26.8	20.1	40
Scrub, tall, closed	3.9	7.2	5.5	11
Scrub, tall, open	3.9	13.4	8.5	17
Herbaceous	28.5	3.1	16.1	32
Barren	46.1	5.2	26.1	52
TOTAL	100.0	100.0	100.0	
# Random Points	102	97	199	199

Table 2. Percentage of each terrain feature observed at random points within the McKinley Slope grizzly bear study area, Denali National Park and Preserve, Alaska, August 1994.

Terrain Feature	> 3,000 ft	≤ 3,000 ft	Combined	# Random Points
River bar	4.9	13.4	9.0	18
Flat	14.7	53.6	33.7	67
Rolling terrain	11.8	21.7	16.6	33
Gentle slope (< 30 degrees)	37.2	10.3	24.1	48
Steep slope (30-60 degrees)	31.4	1.0	16.6	33
TOTAL	100.0	100.0	100.0	
# Random Points	102	97	199	199

30.2, Table 3) with 61% of the population marked. Sight-ability of both females and males was high during the fall survey (60.7 % and 86.2%, respectively). The bounds on the density estimate averaged 9% of the mean after 3 repetitions. The survey area included large glaciers, extensive unvegetated river bars, and substantially more unvegetated habitat above 1,500 m elevation than other studies in the Alaska Range (Miller et al. 1997). Reducing study area size to reflect forage-producing habitat resulted in an adjusted density of 34.7 bears/1000 km² (95% C.I. = 32.2 to 38.7).

Sex and Age Structure. In 1995, the Denali subadult population was 21% males while 36% of adults were male. The male age structure was unimodal (Fig. 2), was 10% subadults, and

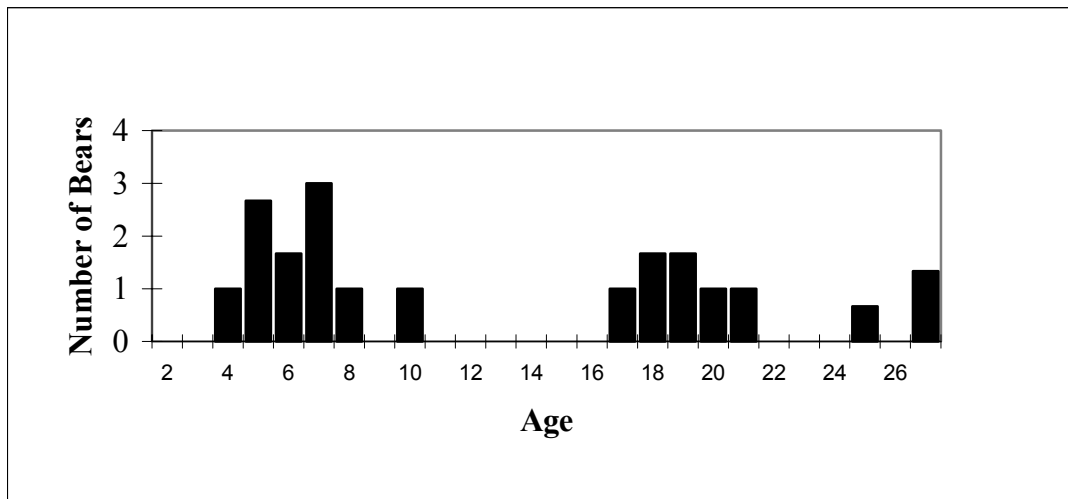
included adults up to 16 years of age. The average age of all independent male bears was 8.9 years and the average age of adults was 9.5 years. The female age structure was strongly bimodal (Fig. 2) and 20% were subadults. The female segment experienced a shift in age distribution between 1991 and 1997 (Fig. 3); each mode advanced 6 years but remained intact. There were 14% subadults in the 1991 female population and 3% in the 1997 population.

Survival Rates. Cubs-of-the-year experienced the lowest annual survival rates at 0.341 (95% C.I. = 0.242 to 0.440, $n = 37$ bear-years, 88 bears). Yearling survival was 0.455 (95% C.I. = 0.284 to 0.627, $n = 21.4$ bear-years, 37 bears) and that of dependent 2-year-olds was

Table 3. Grizzly bear density on the McKinley Slope grizzly bear study area, Denali National Park and Preserve, Alaska, September 1995.

Replication	Dates	Marked Bears Present	Marked Bears Seen	Total Bears Seen	Marked Bears in Area at Least Once	Sightability
1	Sep 23, 24	29	18	33	30	62.1%
2	Sep 25, 27	28	20	34	30	71.4%
3	Sep 28, 30	28	21	30	30	75.0%
TOTAL		85	59	97		69.4%

a)



b)

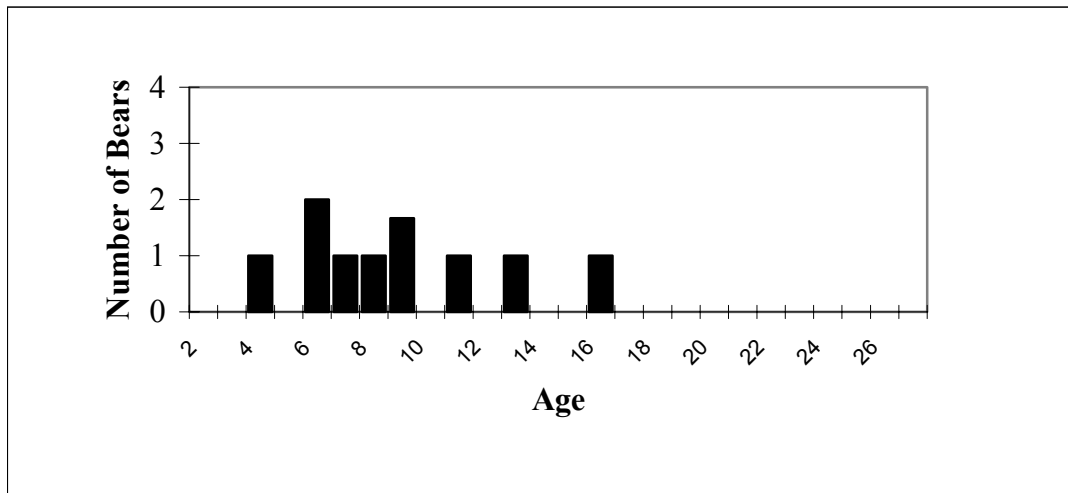


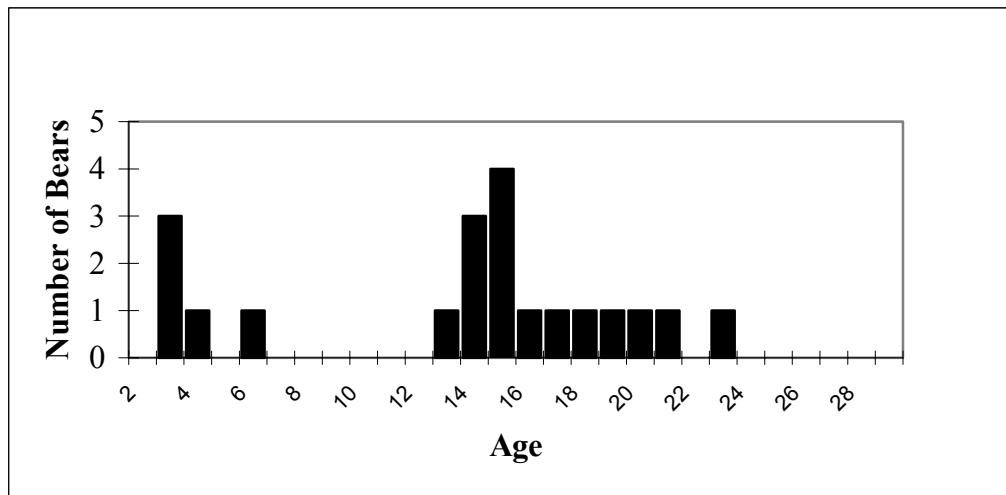
Figure 2. Age structure of female (a) and male (b) grizzly bears on the McKinley Slope study area, Denali National Park and Preserve, Alaska, 1995.

0.785 (95% C.I. = 0.598 to 0.972, $n = 15.2$ bear-years, 22 bears). No mortality was observed among 13 dependent 3-year-olds observed for 5.3 bear-years. Subadult female survival was 1.000 ($n = 21.3$ bear-years, 16 bears) and that of subadult males was 0.943 (95% C.I. = 0.821 to 1.005, $n = 28.7$ bear-years, 20 bears). Adult survival rates were 0.970 (95% C.I. = 0.930 to 1.000, $n = 125.2$ bear-years, 29 bears) for females and 0.983 (95% C.I. = 0.947 to 1.013, $n = 58.6$ bear-

years, 21 bears) for males.

Two males died of natural causes; one 5-year-old was killed by an adult male grizzly bear and a 4-year-old died in mid-summer but the specific cause was undetermined. One adult male, in poor physical condition, was killed in defense of life and property. Three adult females died of unconfirmed natural causes. A 19-year-old had 3 cubs-of-the-year at the time of death, was consumed by another bear, and may have died defending them. An

a)



b)

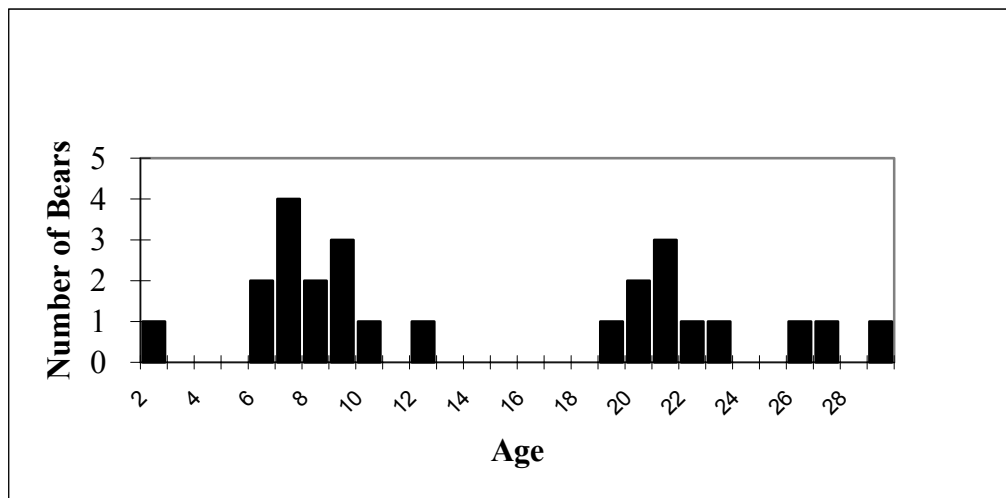


Figure 3. Age structure of female grizzly bears during 1991 (a) and 1997 (b) on the McKinley Slope study area, Denali National Park and Preserve, Alaska.

18-year-old was also consumed by another bear; it was solitary and her bone marrow was 73.9% fat, suggesting poor physical condition. The specific cause of one 20-year-old female was undetermined. The cause of death of one cub-of-the-year was determined to be a crushed skull when the animal was caught in a snow avalanche. It's sibling disappeared simultaneously and may have been buried in the avalanche. Three yearlings died in the den of starvation and were consumed by their

mother at the time of den emergence. Remains of 3 dependent 2-year-olds, all females, showed they had been consumed by bears. The bone marrow from one of them was red and gelatinous indicating the animal was in very poor physical condition at the time of death. Marrow from one of the others was 90.8% fat. Four uncollared males, not included in the above calculations, dispersed from the study area and were legally killed by sport hunters outside the park.

Reproduction. Average age of first reproduction was 7.6 years ($n = 69$ bear-years and 13 bears) and varied from 6 to 10. Two of the 13 females monitored had not produced first litters by 1998. Only 2 females produced first litters that survived to family break-up. Two other young females were accompanied by surviving COY through 1998. Assuming all remaining young adult females produce surviving litters in 1999, the average minimum age of females producing surviving litters would be 10.3 years, but will most likely be higher.

Litter size of cubs-of-the-year at the time of den emergence averaged 2.1 ($n = 42$ litters). Annual litter size varied from 1.9 to 3.0 cubs. Litter size of yearlings at den emergence averaged 1.7 ($n = 20$ litters); annual yearling litter size varied from 1.0 to 2.0. The litter size for 2-year-olds averaged 1.5 ($n = 15$ litters) and varied annually from 1.0 to 2.0. Dependent bears separated from their mothers at an average age of 2.9 years ($n = 19$, $SD = 0.57$). Actual age varied from 2 to 4 years. Reproductive rates were 0.091 for 6-year-olds, 0.306 for bears 7 to 9 years old, 0.384 for bears 10 to 26, and 0.071 for bears 27 to 30 years of age (Table 4).

Population Growth Rate. Three breeding-age females, aged 18 to 20 years, died during the 8-year study. All 3 were reproductively active. Two other females lived to exceed the years of reproductive contribution. Nine bears were observed as subadults and subse-

quently recruited into the breeding population. Two females, first observed as adults, were known to have produced their first litters during the study. The loss of 5 breeding females and gain of 11 suggests an increasing population. In contrast, observed survival and reproductive rates yield a finite rate of increase of 0.977, that of a population declining at about 2% per year.

Table 4. Age specific reproductive rates of radio-collared female grizzly bears, McKinley Slope study area, Denali National Park and Preserve, Alaska, 1991 through 1998.

Female Age	No. of Females Monitored	No. of Cubs	Female Cubs	Female Cubs per Female
6	11	2	1.0	0.0909
7	13	9	4.5	0.3462
8	11	8	4.0	0.3636
9	7	2	1.0	0.1429
10	5	9	4.5	0.9000
11	2	0	0.0	0.0000
12	1	0	0.0	0.0000
13	1	0	0.0	0.0000
14	3	0	0.0	0.0000
15	6	10	5.0	0.8333
16	7	3	1.5	0.2143
17	5	6	3.0	0.6000
18	8	7	3.5	0.4375
19	10	8	4.0	0.4000
20	9	7	3.5	0.3889
21	8	0	0.0	0.0000
22	7	5	2.5	0.3571
23	5	2	1.0	0.2000
24	4	5	2.5	0.6250
25	2	0	0.0	0.0000
26	3	4	2.0	0.6667
27	3	0	0.0	0.0000
28	2	1	0.5	0.2500
29	1	0	0.0	0.0000
30	1	0	0.0	0.0000
Total	135	88	44.0	

Physical Condition. Both subadult and adult males had more body fat during September than in May ($P = 0.001$ for subadults and 0.000 for adults, Table 5). They did not differ from each other during fall ($P = 0.881$). Subadult males did have less body fat than adult males during spring ($P = 0.001$). Similarly, females of both age classes had more body fat during September than in May ($P = 0.000$). They did not differ from each other during either season ($P = 0.292$ for fall, $P = 0.534$ for spring). Adult females that produced cubs may have had more body fat the previous fall than females that did not, although, a larger sample of females without cubs is necessary ($P = 0.134$, $\bar{x} = 26.0$, $n = 7$ for females that were not observed with cubs and $\bar{x} = 29.6$, $n = 25$ for females with cubs). Adult females observed with COY weighed more during the preceding September than eligible females that were not observed COY ($P = 0.036$, $n = 25$ with cubs and 7 without, Table 6). Females aged 5 to 27 that were weighed during a fall and subsequent spring lost an average of 30% total body weight ($SD = 8.40$, $n = 13$) and 18% lean body mass ($SD = 7.67$, $n = 13$). Females aged 5 to 29 captured during a spring and fall of the same year gained an average of 36% of their fall body

weight ($SD = 7.710$, $n = 31$) and 20% of their fall lean body mass ($SD = 9.994$, $n = 26$).

Population Monitoring

Aerial Surveys. The first efforts to develop field methods to measure visibility bias began with 2 days of flying in May 1993. Six of 11 bears were observed during survey flights under very poor sighting conditions. Monitoring aircraft followed survey aircraft, but movements of bears between flights prohibited determination of important sighting conditions for bears not detected by survey aircraft.

More intensive efforts were scheduled in conjunction with a multi-aircraft bear density estimate during September 1994 but inclement weather precluded completion of field work. During one day of flying, 10 of 10 marked bears were detected by survey planes. Sighting conditions that day were ideal with 4 to 6 inches of fresh snow throughout the study area.

During September, 1995, we tested 2 methods of obtaining sighting conditions of bears missed during survey flights. On the first day we radio tracked in survey units before and after survey flights to provide 2 known locations of each bear to test for movement. Movements between locations were high so we next used high altitude surveillance simultane-

Table 5. Percent body fat of grizzly bears of different age classes during each season, McKinley Slope study area, Denali National Park and Preserve, Alaska, 1991 through 1998.

Sex	Age Class ^a	Season	Percent				
			Fat	n	SD	Minimum	Maximum
Female	Adult	May	8.3	37	4.100	2.0	17.0
Female	Adult	September	27.4	52	6.237	16.0	47.0
Female	Subadult	May	7.3	8	4.136	2.0	14.6
Female	Subadult	September	25.1	10	5.466	18.0	33.0
Male	Adult	May	14.5	21	3.773	8.0	24.0
Male	Adult	September	23.2	7	4.282	18.0	31.0
Male	Subadult	May	8.3	13	5.801	-4.0	17.0
Male	Subadult	September	23.8	6	10.572	12.0	40.0

^a Adults were ≥ 6 years, subadults were independent and ≤ 5 years.

Table 6. Weights (kg) of grizzly bears of different age classes during each season, McKinley Slope study area, Denali National Park and Preserve, Alaska, 1991 through 1998.

Sex	Age Class ^a	Season	Mean Age	Mean Weight	n	SD	Minimum	Maximum
Female	Adult	May	16.4	99.2	59	13.403	69.0	132.0
Female	Adult	September	14.2	154.3	53	20.590	115.0	203.0
Female	Subadult	May	3.9	72.0	16	15.476	47.5	96.0
Female	Subadult	September	4.1	135.8	13	17.574	104.0	172.0
Female	COY	May	0.0	5.0	3	1.732	4.0	7.0
Female	COY	September	0.0	28.5	4	2.380	25.0	30.0
Male	> 9 years	May	16.7	205.1	20	38.022	146.0	260.0
Male	> 9 years	September	18.0	201.5	2	10.607	194.0	209.0
Male	Adult	May	13.2	189.1	32	44.068	104.0	260.0
Male	Adult	September	9.5	194.6	8	16.062	163.0	213.0
Male	Subadult	May	4.1	92.5	30	25.238	48.0	159.0
Male	Subadult	September	3.9	136.7	10	32.857	96.0	195.0
Male	COY	May	0.0	7.3	3	0.577	7.0	8.0
Male	COY	September	0.0	25.0	3	5.568	19.0	30.0

^a Adults were ≥ 6 years, subadults were independent and ≤ 5 years, COY refers to cubs-of-the-year.

ous to survey flights. Survey planes detected 14 of 21 bears monitored. Difficulties for high surveillance aircraft included inability to continuously observe bears in some habitats and uncertainty about when survey aircraft should have detected a bear, especially when multiple passes were made near the bear. These issues were important since sight-ability conditions varied with bear movement, cloud cover, and aircraft position, all of which could change in a short period of time.

Four experienced biologist/pilot teams correctly classified 69% of a blind sample of marked bears as adult female, adult male, subadult female, or subadult male ($n = 59$). When subadult sexes were combined, classifiers were correct 73% of the time. The most experienced biologist correctly classified 81% of observations.

Thermal Infrared Imaging. Thermal infrared temperatures were obtained from 55

bears during 1995 through 1998. Visual inspection of data suggests that for overcast conditions, bear surface temperatures were about 6 to 8 C higher than background temperatures. Under high incident solar radiation, however, bear surface temperatures can exceed that of the background by as much as 56 C and can vary by 50 C on the bear itself.

DISCUSSION

Population Ecology

Serum antibody prevalence for infectious canine hepatitis, canine distemper, and leptospirosis was similar to or lower than elsewhere in Alaska (Zarnke and Evans 1989, Zarnke 1992). Zarnke and Evans (1989) used a threshold titer level of 1:20 for infectious canine hepatitis. At that level only 1 Denali grizzly bear would have been considered positive instead of 3. This low prevalence makes it unlikely that disease was a significant factor affecting grizzly bear cub survival during the

study.

Brown bear density in Denali National Park, adjusted to represent forage-producing habitat, was comparable to those reported by Dean (1987) and Murie (1981) on adjacent study areas in the Park. It was higher than the nearby harvested Susitna population during 1985 (Miller et al. 1997). Sight-ability of both females and males was higher during the fall Denali survey than reported in other areas of Alaska (Miller et al. 1997). High sight-ability of both sexes during fall density estimates was due to greater activity of bears during the period of hyperphagia as compared to spring surveys (Stelmock and Dean 1986), and open nature of habits used for foraging at that time. Sight-ability was sufficient to markedly reduce survey costs to obtain an adequate sample for density estimation in areas where fall hunting season does not compromise human safety or the vulnerability of study animals to sport harvest due to aircraft attention or disturbance.

The bimodal distribution of the female population likely resulted from periodic recruitment related to high dependent bear mortality. Pulses of recruitment probably occur either when foraging conditions become exceptional or predation eases due to unknown factors.

High density, high independent bear survival rates, and lack of human interference during the past 80 years suggests the Denali population is likely at carrying capacity. High dependent mortality coupled with periodic recruitment may allow the population to oscillate mildly around a mean density, but in the long term, the population is likely stable. The negative rate of increase associated with observed survival and reproductive rates is probably a result of the study not monitoring cub production and survival long enough to include a recruitment pulse.

During the brief summer months, adult females gain about 50% of their spring weight in preparation for cub production and the long

winter hibernation. The loss of 18% to 20% lean body mass during winter comes largely from skeletal muscle and emphasizes the marginal nutritional condition of females and subadult males in this population. Starvation loss and poor physical condition associated with some dependent bear mortality suggests that nutrition plays a role in the high mortality rates of dependent bears.

Population Monitoring

Aerial Surveys. Fall surveys provided the highest sight-ability and minimized potential observation bias due to habitat selection and secrecy among bears of differing sex and reproductive status, compared to spring surveys in similar habitats (Miller et al. 1997). Fall surveys are not bias-free, however, since more detection bias was observed between individuals within rather than among sex and reproductive groups (Miller et al. 1997). Without some means to measure or correct for sight-ability bias there will always be uncertainty when comparing surveys between locations and years, as sighting conditions vary.

None of the methods we tested for measuring sighting bias proved satisfactory. Simultaneous, high altitude surveillance was most promising but still did not permit accurate determination of sighting conditions of missed bears at the desired scale. Coarser scale studies, using detection rates in broad vegetation categories, may have been possible but the loss of information and precision in estimating the number of missed bears was a concern. Inability to develop clean and efficient sampling procedures resulted in abandonment of efforts to measure visibility bias following field work in 1995. Continued research on double sampling techniques by Dr. Earl Becker (Alaska Department of Fish and Game) may prove helpful, but limitations due to low bear density at Denali will likely be a concern.

High observed mortality rates of dependent

bears and high between year variability in production suggests that monitoring cub production and survival from radio-collared bears would only be valuable in extremely long-term studies with reasonable conclusions drawn about each decade. The high expense of such efforts for the amount of information received makes it impractical.

Alternatively, existing data could be used to estimate a range of possible variances for the binomial estimator. Modeling efforts could display the range of precision likely under varying conditions. If this technique appears favorable, it should be validated on a known density population. Then, traditional aerial surveys using the binomial estimator, bears per square kilometer or bears per hour, would provide useful estimates where bears are not harvested and human impacts not expected. When the need for precise information regarding population status is great, intensive, short-term capture-mark resight studies using radio transmitters are recommended.

Thermal Infrared Imaging. Bear surface temperatures appeared sufficiently different from background temperatures to permit detection using currently available thermal infrared equipment, during periods of overcast skies or during early morning or late evening hours when incident solar radiation is at a low angle. Confirmation of these findings through more rigorous quantitative analysis, coupled with a theoretical assessment of survey height, survey path, image size, and observation procedures, for the terrain bears inhabit in Denali National Park, should be accomplished prior to conducting additional field work. The expense of this technique, given the current availability of equipment, plus the research and development necessary to make this technique operational, will limit its value in the near term as a useful bear population monitoring tool. Even if in the long term it does not provide improved detection rates the fact that biases

associated with it differ from those associated with visual surveys suggests it may still have promise as a supplemental tool or to validate other techniques. Consequently, development of the technique should be supported but only if the cost of development can be maintained at reasonably low levels. Development should occur at locations proximate to available thermal infrared equipment.

MANAGEMENT RECOMMENDATIONS

1. *Conduct intensive, short-term studies of grizzly bears in different habitats within and around the park to 1) determine population status at additional locations, and 2) identify human factors that could affect grizzly bear productivity or survival. Monitor those human factors and important natural resources that could be affected by humans.* Continuous monitoring of long-lived, low density animals with low reproductive output is too expensive for most monitoring programs. Understanding ecological requirements of those animals and the potential impacts human activities might have on them would provide a means to monitor causative factors at much reduced cost. These studies would provide valuable baseline data needed for future comparisons to document whether change has occurred.

2. *Use global positioning system and geographic information system technologies to determine grizzly bear habitat use patterns and build a comprehensive model of prioritized bear habitats which would identify potentially important movement corridors and foraging habitats in areas likely for human development or activity.* Models could predict the area and proportion of various qualities of habitat that would be affected by human activities, without the complexity of attempting to quantify impacts to carrying capacity or population dynamics.

3. *Use global positioning system and geographic information system technologies to assess impacts of various human activities on bear movements and use those data to enhance the habitat model.* The habitat quality model could be fine-tuned to assess the amount of impact based on the type and amount of human activity proposed. Much of this work can be drawn from studies outside Denali, although some effort to elucidate impacts of human activities unique to Denali may be necessary.

4. *Conduct periodic autumn aerial surveys, without marked bears, using the binomial estimator, bears observed per hour and bears observed per square kilometer, to provide a measure of bear distribution, abundance, status, and to determine important concentration areas, for occasional evaluations where human influence on the population is expected to be negligible, or when first considering an area for intensive study.* This technique is least expensive and least intrusive on the bear population, can be accomplished during one field season, and can be implemented immediately. Highly experienced pilots and observers can provide a reasonable assessment of sex and age composition to suggest a healthy population. Unexpectedly low bear observation rates or a low proportion of dependent bears would be cause for more intensive investigation.

5. *Conduct intensive surveys, using radio collars and capture-mark-resight techniques, when there appears to be a change in factors that affect bear reproduction and survival, for harvested populations, or when new developments pose threats to an existing population.* When more precise, unbiased data are needed for comparisons between populations or between years, capture-mark-resight techniques provide the only reliable and proven method. Such effort will require two to three years of pre-marking to assure all reproductive classes of adult females are represented in the

marked population for the density estimate. Such efforts could efficiently be combined with other recommendations for concurrent study.

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