

Reproduction and survival of brown bears in southwest Alaska, USA

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Abstract: From June 1993 to June 2003, 40 adult female brown bears (*Ursus arctos*) were captured, radiocollared, and tracked for 1 to 10 years in a previously unstudied population in southwest Alaska. Mean litter size upon emergence from dens was 2.0, decreasing to 1.5 at weaning. Mean age of offspring at weaning was 2.9. Mean age of primiparity was 7.2 years while first weaning was estimated at 9.5 years. Mean maximum age of a female weaning a litter was 27.3 years. Mean annual survival estimates were 90.1–97.2% for radiocollared females ≥ 5 years old, 48.2–61.7% for cubs of the year, and 73.3–83.8% for 1 and 2-year-old offspring combined. Of 129 offspring followed beginning with their first summer, 38 (29.5%) survived to be weaned. Hunters harvested at least 12 marked or radiocollared bears (9 males and 3 females). No defense of life and property (DLP) killings were reported within or near the study area, but illegal harvests of brown bears were known to have occurred in the general region. Harvests within or near the study area averaged 7.3–12.1 males/year and 4.8–5.2 females/year. This population's rate of increase (λ) was estimated as 1.035–1.047 for the first half of the study, 0.963–0.997 for the second half, and was found to be most sensitive to survival of females 5–14 years old.

Key words: Alaska, brown bear, grizzly bear, lambda, mortality rate, rate of increase, reproduction, survival, *Ursus arctos*

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During the early 1990s, native groups representing subsistence hunters in southwest Alaska petitioned federal land managers under the provisions of the Alaska National Interest Lands Conservation Act (Public Law 96-487) and the Alaska Board of Game to increase harvest regulations for brown bears (*Ursus arctos*) to more closely reflect customary and traditional practices (Van Daele et al. 2001). As a result, both federal and state subsistence bag limits were increased from 1 bear/4 years to 1 bear/year. This study was initiated to estimate basic biological parameters for establishing sustainable harvest levels and developing methods to monitor brown bears in the Kuskokwim Mountains. Van Daele et al. (2001) described the original study objectives and presented preliminary findings.

Our primary objective was to determine if the brown bear population could withstand the increased harvest that might result from liberalized subsistence harvest regulations. We report the results for the study's primary objective, including basic biological parameter estimates, and discuss harvests during the study.

Study area

The study area was located in the southwest Kuskokwim Mountains, midway between Dillingham and Bethel, Alaska (Fig. 1; approximately 60°N, 159°W; see Van Daele et al. 2001 for details). It encompassed approximately 7,800 km² of public lands (as estimated *a posteriori* from 99% of all locations from radiocollared bears) of the Yukon Delta National Wildlife Refuge (YDNWR) (48%), Togiak National Wildlife Refuge (TNWR) (19%), and Alaska State lands (33%). There were no roads, private in-holdings, or permanent structures in the study area. Primary human use was hunting, fishing, and recreation.

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Elevations ranged from 75 m in the western portion of the study area (tundra plains) to 1,534 m (glacial peaks). The study area included the hydrographic divide between the Nushagak River to the east, the Togiak River to the south, and Kuskokwim River watersheds to the north and west. Mean annual precipitation was 89 cm, including 177.5 cm of snow. Snow persisted in lower elevations from late October to May; vegetation developed rapidly during the short growing season. Mean maximum and minimum temperatures for January were -10.5°C and -16.5°C , and for July were 18.5°C and 7°C , respectively (National Weather Service files, Bethel, Alaska, USA).

Subsistence use of the study area declined from 1991 through 2003. Local villagers typically established seasonal camps each spring to harvest arctic ground squirrels (*Spermophilus parryii*) and brown bears; however, the number and duration of these camps diminished through time (personal observation). Some accessed fall caribou (*Rangifer tarandus*) hunting and berry picking sites within the study area with chartered aircraft; snow machines were used for hunting caribou in winter and bears in spring. Spring bear hunting activities, as measured by number of camps observed, appeared to decline during the study period (Kovach, unpublished data).

Methods

Bears were captured, measured, and radiocollared in 1993, 1994, 1997, 2000, and 2003 following Van Daele et al. (2001); radiocollars were deployed on bears ≥ 4 years old. Flights to locate radiocollared bears occurred bi-monthly between April and November when bears were likely to be out of their dens, monthly when they were in their dens.

Captured bears were aged by cementum aging (Mundy and Fuller 1964, Matson et al. 1993). Ages of 161 offspring were determined from known birth year and visually estimated for 16 offspring. A cub was defined as a bear in its first year of life; an adult was defined as a bear ≥ 5 years old. Age of primiparity was calculated using female bears that were 4–6 years old at radiocollar deployment; only one was accompanied by offspring when initially captured. Age of first weaning, defined as the age of the female when producing the first litter to be weaned, was calculated using bears that were < 9 years old at collar deployment and accompanied by older offspring; this was based on a *posteriori* analysis that showed the youngest female to produce cubs that survived to weaning was 7 years old. Intervals

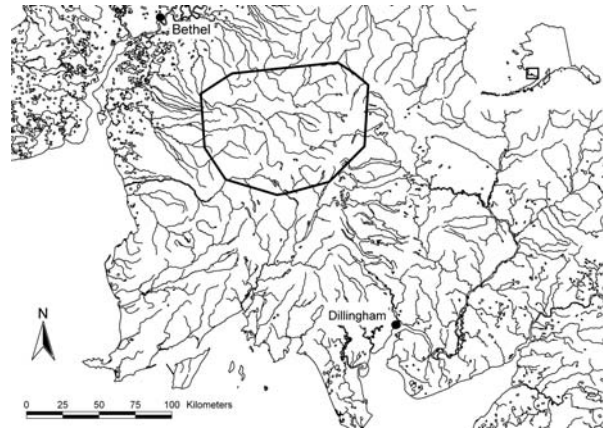


Fig. 1. Brown bear study area (outlined) in the southwestern Kuskokwim Mountains, Alaska.

between weanings for radiocollared females were projected following Craighead et al. (1995:61), as was estimated mean time between weaning litters. Inter-birth interval was defined as the time between cub litters (Eberhardt et al. 1994, Case and Buckland 1998). Weaning interval was defined as the time between successful weanings (Reynolds and Hechtel 1983, Schwartz and Franzmann 1991, Reynolds 1997). Offspring were considered weaned if they were ≥ 2 years old and were not observed traveling with the radiocollared female by late June.

Mortalities of radiocollared bears were confirmed by ground inspection at the radiocollar location. Mortalities of offspring of radiocollared females were inferred from lack of direct observation for ≥ 3 consecutive flights, or from behavior of the female. If a female died while accompanied by cub or 1-year-old offspring, we assumed they also died. Two females died late in the year while accompanied by 2-year-old offspring. Due to uncertainty of the fate of those offspring, they were censored from offspring survival calculations.

Survival of offspring to weaning was calculated by observing litters beginning in the spring of their birth year through weaning. Mean litter sizes were determined from litters observed in the spring of their birth year (i.e., litter size at den emergence); mean weaned litter size was determined from litters considered weaned. Survival of offspring after weaning was not investigated.

Survival estimates were calculated with the staggered entry design of Pollock et al. (1989) in Excel (version 2002, Microsoft Corp., Redmond, Washington, USA). Mean annual survival rate was calculated by taking the n^{th} root of the final estimate (Amstrup and Durner 1995).

Sample sizes forced merging 1- and 2-year olds for survival rate calculations. Timing of offspring losses was estimated using the midpoint between the last date observed and the first date offspring were absent. Data from Alaska Department of Fish and Game (ADFG, Anchorage, Alaska, USA, unpublished data) were used to estimate harvest mortalities of non-radiocollared bears. Due to harvest location reporting and coding, some uncertainty existed when determining if a bear was harvested within the study area. Therefore, harvest locations were classified as out of the study area, within the study area, or potentially within the study area; only those classified as within ($n = 83$) or potentially within ($n = 8$) the study area were used for evaluating harvest. Harvest rate of marked bears was not calculated because only females were sought for capture after 1994, and very large males were avoided during capture efforts in 1993 and 1994.

We assumed a 50:50 sex ratio at birth (Eberhardt et al. 1994). A stable population structure is assumed by the Leslie matrix model (Leslie 1945) used to estimate population growth rate, lambda (λ ; Gilbert and Udevitz 1997). Lambda was estimated with a full Leslie matrix model using the PopTools (Hood 2004) add-on for Excel using averaged reproductive and survival rates for bears >4 years old and age-specific survival for bears ≤ 4 years old. In an attempt to assess the effects of increasing age, we created equally spaced age classes for bears >4 year old (i.e., 5–9, 10–14, 15–19, 20–24, and 25–29 yrs old); however, sample size limitations forced merging the 20–24 and the 25–29-year-old classes. Lambda was calculated with age-specific survival rates for bears ≤ 4 -years-old as before, and mean reproductive and survival rates for the 4 age classes for bears >4 years old.

We calculated reproductive rate (number of female cubs/adult female/yr) following McLellan (1989a; McLellan method) and Eberhardt (1995; Eberhardt method); the former method weights each female based on the time it was observed, whereas the latter produces a population average. We calculated λ using both values. The Leslie matrix was constructed following the post-breeding census method of Akçakaya et al. (1999), in which fecundity is calculated by multiplying the age-class reproductive rate by the age-class survival rate. Elasticity (i.e., proportion of the sensitivity to small changes) was calculated for both reproduction and survival using PopTools.

Jackknife procedures (Caswell 1989) were used to obtain a variance for λ , from which confidence intervals were calculated. Temporal changes in reproductive

rates, survival rates, and λ were investigated by analyzing 3-year means using *K*-means clustering with Euclidean distances (Hartigan 1975, SPSS 1999). This led to assessing changes in reproductive rates, survival rates, and λ values between the first half (i.e., 1993–97) and the second half (i.e., 1998–2002) of the study. Differences in reproductive rates, survival rates, and λ between periods were tested as follows: using only bears observed in both periods, jackknife estimates were calculated for each parameter each period; the difference in estimates from each jackknife iteration was calculated; these jackknifed differences were used to estimate the variance of the parameter's difference between periods and its confidence interval; confidence intervals that did not contain zero demonstrated significant differences in a parameter between periods. Difference in litter sizes between periods was tested using a Mann-Whitney test. Statistical tests were performed using SYSTAT (version 10.0, SPSS, Inc.) and SPSS (version 10.0, SPSS, Inc.). We assumed significance at $\alpha = 0.10$.

Results

Captures and telemetry

We captured and marked 79 brown bears (27 males, 52 females) 156 times; 44 were outfitted with radiocollars (Model 500, Telonics, Inc., Mesa, Arizona, USA). Due to difficulties in keeping telemetry collars on males in 1993 ($n = 4$; Van Daele et al. 2001), only females were collared in 1994 ($n = 8$) and 2000 ($n = 10$). Existing collars were replaced in 1997 ($n = 25$) and 2000 ($n = 17$); all collars were removed in 2003 ($n = 19$). Captured bears varied from 0.5 to 29.5 years old.

From June 1993 through June 2003, 40 radiocollared females yielded 2,372 unique locations (locations not duplicated, such as dens); females were observed on 72.4% of radio fixes and dependent offspring were observed 770 times. For females followed >3 years ($n = 27$), a mean of 79.7 unique locations/bear (median = 82.0; range = 29–128) were collected over an average of 7.9 years (SD = 2.1; median = 9.0; range = 3.9–10.0); an average of 1 relocation/15 days while bears were out of their dens. Radiocollared females were followed a total of 251 bear years.

Reproduction

From 1993 to 2003, mean size of cub litters upon den emergence was 2.0 (SD = 0.7; range = 1–3; $n = 81$ litters). Mean litter size in the spring for 1-year olds was 1.6 (SD = 0.6; $n = 56$ litters), for 2-year olds was 1.6 (SD = 0.6; $n = 42$ litters), and for 3-year-olds was 1.5

(SD = 0.7; n = 13 litters). Mean age of offspring at weaning was 2.9 years (SD = 0.6; range = 2–4; n = 52 cubs), and mean litter size at weaning was 1.5 (SD = 0.6; range = 1–3; n = 34 litters). Mean cub litter size did not appear to differ between periods (1993–97, \bar{x} = 1.9, SD = 0.6, n = 34 litters; 1998–2002, \bar{x} = 2.1, SD = 0.7, n = 39 litters), nor did mean weaned litter size (1993–97, \bar{x} = 1.8, SD = 0.6, n = 12 litters; 1998–2002, \bar{x} = 1.4, SD = 0.6, n = 21 litters).

Mean age of primiparity, calculated following Garshelis et al. (1998), was 7.2 years (range = 5–9 yrs; n = 17 bears); however, mean age of first weaning was 8.5 years (range = 5–14 yrs; n = 20 bears). The proportion of nulliparous females that produced their first litter at ages 5, 6, 7, and ≥ 8 years was 13%, 20%, 45%, and 100%, respectively. During the study 5 females were censored prior to producing their first litter: 3 died (\bar{x} age = 6.0 years; SD = 1.0; range = 5–7), 1 (age = 7 yrs) had a transmitter failure, and 1 (age = 7 yrs) had her radiocollar removed in 2003. In 2003, 3 females (\bar{x} age = 10.0 yrs; SD = 2.6; range = 8–13) were accompanied by dependent offspring, but had yet to wean their first litter. Assuming those litters survived to be weaned, the mean age of first weaning would be a minimum of 9.5 years; 2.3 years greater than primiparity. Sample sizes were insufficient to assess differences between periods of the study.

We monitored 8 females ≥ 20 years old for 39 bear years; all produced or weaned offspring. Four died of non-human related causes during the study and were used to calculate the maximum age of a female weaning a litter (\bar{x} = 27.3 yrs; SD = 1.5; range = 26–29). The remaining 4 (\bar{x} = 24.3 yrs; SD = 0.5; range = 24–25) were accompanied by offspring (1 with a cub, 3 with yearlings) when their radiocollars were removed in 2003.

We observed 48 inter-birth intervals (\bar{x} = 2.5 yrs, SD = 1.1, range = 1–5, n = 21 bears) and inferred an additional 9 based on estimated ages of dependent offspring (\bar{x} = 3.4 yrs, SD = 0.5, range = 3–4, n = 9 bears). Mean inter-birth interval using all data was 2.6 years (SD = 1.1). We observed 9 weaning intervals (\bar{x} = 4.0 yrs; SD = 1.0; range = 3–6, n = 7 bears), and minimum duration was estimated for an additional 33 intervals (\bar{x} = 4.7 yrs; SD = 1.4; range = 3–8, n = 28 bears). The minimum mean weaning interval (i.e., open cycle of Craighead et al. [1995:61]) was 4.6 years (SD = 1.4). We found no difference in birth interval between periods (1993–97, \bar{x} = 2.6, SD = 1.1, n = 22; 1998–2002, \bar{x} = 2.9, SD = 1.1, n = 27).

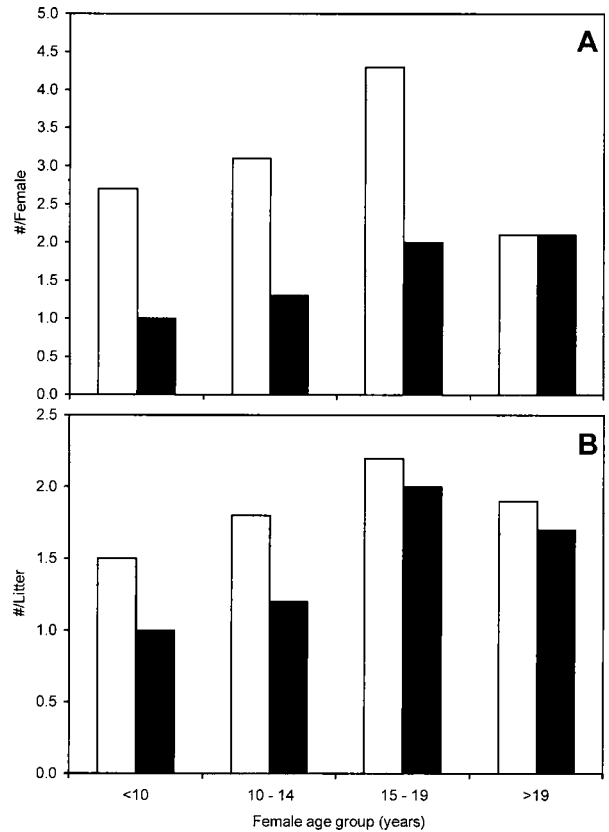


Fig. 2. Production (open bars) and weaning (solid bars) of offspring by age (at time of litter birth and weaning) of radiocollared female brown bears in the southwestern Kuskokwim Mountains, Alaska, 1993–2003, expressed as number/female (A) and number/litter (B). Y-axis scales differ.

For litters followed beginning with their first summer, we evaluated production and weaning success by female age. As females became older, they not only became more successful at weaning offspring (ANOVA F = 1.708, 17 df, P = 0.076; Fig. 2a), but appeared to wean older offspring in larger litters (females <20 yrs old, \bar{x} = 2.9 years old at weaning, SD = 0.5, n = 25 litters, \bar{x} litter size = 1.4, SD = 0.7; females ≥ 20 yrs old, \bar{x} = 3.1 years old at weaning, SD = 0.7, n = 9 litters, \bar{x} litter size = 1.7, SD = 0.5; Fig. 2b).

Although there may have been others, we inferred 3 instances of breeding outside the observed breeding season. Bear 125 lost her 1-year old between 23 July and 27 August 1997; the following spring she was observed with 1 cub. She subsequently lost that cub between 17 July and 3 September 1998 and was observed again with 1 cub in May 1999. In June and July 1998, bear

Table 1. Survival and reproductive rates of radiocollared female brown bears and their dependent offspring from the southwestern Kuskokwim Mountains, Alaska, 1993–2003.

	Survival rates (90% confidence intervals)			Reproductive rates (90% confidence intervals)					
	Mean ^c	1993–1997	1998–2002	McLellan ^a			Eberhardt ^b		
				Mean ^c	1993–1997	1998–2002	Mean ^c	1993–1997	1998–2002
Mean ^d	0.946	0.972	0.910	0.302	0.262	0.329	0.270	0.238	0.296
0 yr	(0.942–0.949)	(0.968–0.976)	(0.903–0.917)	(0.295–0.309)	(0.253–0.271)	(0.318–0.340)	(0.262–0.278)	(0.229–0.247)	(0.284–0.308)
	0.553	0.679	0.482	0	0	0	0	0	0
	(0.530–0.576)	(0.647–0.711)	(0.431–0.533)						
1–2 yrs	0.713	0.838	0.724	0	0	0	0	0	0
	(0.690–0.736)	(0.818–0.857)	(0.689–0.759)						
3 yr	0.874 ^e	0.902 ^e	0.862 ^e	0	0	0	0	0	0
4 yr	0.982	0.967	1.000	0	0	0	0	0	0
	(0.942–0.949)	(0.957–0.977)	(1.000–1.000)						
5–9 yrs	0.988	0.974	1.000	0.262	0.214	0.353	0.228	0.180	0.303
	(0.985–0.991)	(0.962–0.985)	(1.000–1.000)	(0.247–0.277)	(0.198–0.230)	(0.290–0.416)	(0.211–0.245)	(0.162–0.198)	(0.237–0.369)
10–14 yrs	0.947	1.000	0.887	0.321	0.229	0.362	0.255	0.175	0.370
	(0.940–0.954)	(1.000–1.000)	(0.872–0.903)	(0.307–0.335)	(0.191–0.267)	(0.344–0.379)	(0.241–0.270)	(0.136–0.214)	(0.343–0.397)
15–19 yrs	0.955	0.956	0.944	0.378	0.452	0.235	0.377	0.450	0.365
	(0.938–0.971)	(0.930–0.982)	(0.917–0.971)	(0.341–0.414)	(0.371–0.534)	(0.163–0.307)	(0.325–0.429)	(0.364–0.536)	(0.231–0.499)
20–29 yrs	0.939	0.944	0.922	0.273	0.250	0.318	0.268	0.244	0.239
	(0.918–0.960)	(0.880–1.000)	(0.888–0.956)	(0.233–0.313)	(0.182–0.318)	(0.236–0.400)	(0.221–0.316)	(0.180–0.307)	(0.164–0.315)

^aMcLellan (1989a).^bEberhardt (1995).^c1993–2002.^dMean value for all radiocollared bears ≥ 5 years old.^eMean value of 1–2 yrs and 4 yrs.

136 was observed with two 2-year-old offspring and avoiding nearby males. In August 1998, she was observed defending the carcasses of her offspring from the survey aircraft; a large male was observed within 250 m. The following spring she was accompanied by 2 cubs.

Survival and mortality

Mortality sources included human caused ($n = 3$), conspecific interaction ($n = 1$, and possibly 2 others), avalanche ($n = 1$), and unknown but believed to be natural (i.e., non-human caused; $n = 6$). Overall mean annual survival rate for radiocollared females ≥ 5 years old was 91.0–97.2% (Table 1). Overall mean annual survival among adults was significantly higher ($P = 0.017$) for 5–9-year olds, but was not different between the other 3 adult age classes (Table 1). *K*-means cluster analysis (F -ratio = 50.35) of the 3-year means (Fig. 3a) indicated that survival in the first half of the study was higher than in the second.

Offspring losses were not evenly distributed temporally ($\chi^2 = 33.459$, 10 df, $P = 0.000$) May–October (Fig. 4). Mortality sources to offspring were largely unknown; accidents such as falls in steep rock and cliff areas and drowning in snow-melt flooded streams in early summer were suspected as contributing mortality sources. Based on the proximity of males to radiocollared females

accompanied by offspring and the subsequent loss of those offspring, we inferred 2 cases of infanticide: bear 136's loss in 1998 described above, and bear 172's loss of 2 cubs between 4 June and 6 June 2003.

Of 129 offspring (65 litters) followed beginning with their first summer, 38 (29.5%) from 25 litters survived to weaning. For 1- and 2-cub litters, females that lost entire litters were younger than females that retained part or all of their litters (Table 2); this pattern did not hold for 3-cub litters, however. Partial loss of cub litters declined from the first half of the study (29%, $n = 10$ litters) to the second half (15%, $n = 6$ litters); loss of whole cub litters increased through time (1993–97, 21%, $n = 7$ litters; 1998–2002, 38%, $n = 15$ litters). We lacked sufficient sample sizes to determine if both of these differences were real or were by chance. Overall mean cub survival was significantly higher ($P = 0.095$) during 1993–97 (67.9%) than 1998–2002 (48.2%); survival of older offspring was also significantly higher ($P < 0.001$) during 1993–97 (83.8%) than 1998–2002 (72.4%; Table 1).

Sport hunters reported harvesting 9 marked males, 1 marked female, and 2 radiocollared females between fall 1993 and fall 2002. Most ($n = 10$) occurred within the study area. Sport hunters reported an additional 79 brown bears (51 males, 27 females, 1 sex unrecorded) harvested within or potentially within the study area during this period (Fig. 5). Between autumn 1993 and

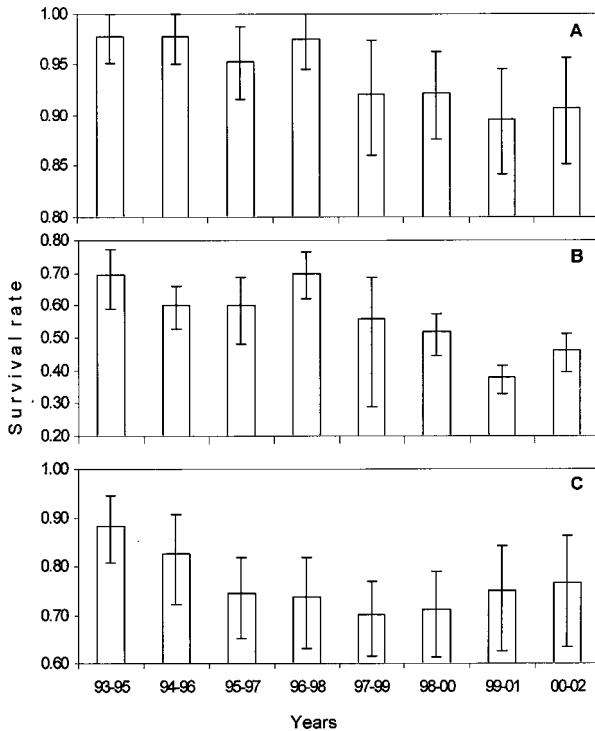


Fig. 3. Mean (with 90% confidence interval) survival of radiocollared female brown bears (A), cubs (B), and 1- and 2-yr-old dependent offspring (C) of radiocollared females in the southwestern Kuskokwim Mountains, Alaska, 1993–2002. Y-axis differs between age groups.

autumn 2000, sport hunters harvested 7.9 bears/year. Spring hunts accounted for 26 kills (2.7 males/yr, 1.0 females/yr) and fall hunts for 33 (2.8 males/yr, 1.4 females/yr). From spring 2001 through fall 2002, there was an increase in the number of bears reported by sport hunters (12 spring harvests, 5.0 males/yr, 1.0 females/yr; 20 fall harvests, 5.0 males/yr, 5.0 females/yr). Further, the male:female ratio in the reported harvest increased through the 1998–2000 mean then declined as harvest increased (Fig. 5).

Non-resident sport hunters were required to use a guide for brown bear hunting throughout Alaska and to have their harvest inspected and sealed. As 79% of the sport harvest was taken by guided hunters and another 10% by hunters from urban areas of Alaska (ADFG, Anchorage, Alaska, USA, unpublished data), we believed that reporting by sport hunters was high. Of the 30 female bears reported by sport hunters, 22 (73%) were aged by ADFG personnel and all were ≤ 12 years old; 48 of the 60 males had ages determined and 40

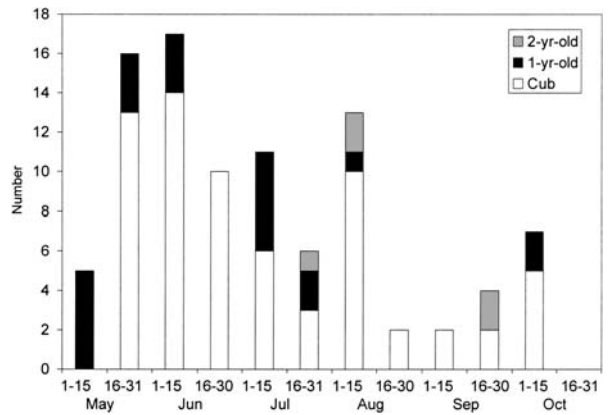


Fig. 4. Timing of dependent offspring lost by radiocollared female brown bears in the southwestern Kuskokwim Mountains, Alaska, 1993–2003.

(83%) were ≤ 15 years old (ADFG, Anchorage, Alaska, USA, unpublished data).

Subsistence hunters did not report harvesting any marked or radiocollared bears during the study. However, village elders indicated a small probability of reporting such a take (S.D. Kovach et al., 2003, Brown bear density, movements, and population parameters in the southwestern Kuskokwim Mountains, Alaska—1996–2000 progress report, US Fish and Wildlife Service, Bethel, Alaska, USA). Little data exist on subsistence harvests from the study area as harvest locations are rarely reported; additionally, sex is not always reported and harvested bears are not aged (ADFG, Bethel, Alaska, USA, unpublished data).

Beginning in fall 1992, subsistence brown bear hunters were required to obtain a free registration permit and complete a mail-in survey at the end of the hunting year (Jul–Jun) rather than purchase a permit and have their harvest inspected (Van Daele et al. 2001). Between fall 1991 and fall 1994, we tested the reporting rate of registration permit holders throughout the region from interviews with subsistence hunters (C. Hensel, unpublished reports to US Fish and Wildlife Service, Bethel, Alaska, USA: 1994, Brown bear harvests in the Western Alaska Brown Bear Management Area, 1992/1993: Statistical information and cultural significance, results of the AVCP harvest survey of October–December 1993; and 1995, Brown bear harvests in the Western Alaska Brown Bear Management Area [WABBMA], 1993/1994: Statistical information and cultural significance, results of the AVCP harvest survey of March–May; J. Andrew and T. Brelsford, 1993, Brown bear use in the Western Alaska Brown Bear

Table 2. Offspring losses by initial litter size and female age (median age at time of litter birth) for radiocollared females from the southwestern Kuskokwim Mountains, Alaska, 1993–2003.

Litter size	Lost			Female age
	Offspring	Litters	%	
1	0	4	27	12
	1	11	73	9
	0	9	26	14
2	1	7	20	11
	2	19	54	10
	0	1	7	13
3	1	2	14	12
	2	2	14	10
	3	9	64	13

Management Area, results of the AVCP survey of September–October 1992, report to US Fish and Wildlife Service, Bethel, Alaska, USA). The interviews reported 350% more harvests (344% more fall harvests and 366% more spring harvests) than mail-in surveys (Table 3). Interviews indicated that 25 brown bears (18 males, 7 females) were harvested by subsistence hunters from within or potentially within the study area at an average rate of 5.1 males/year and 2.0 females/year (Table 3). Although no additional interview data were collected after 1994, we believe that the pattern of non-reporting by subsistence hunters continued throughout the study. During fall 2002, 2 brown bears were known to have been harvested without permits (M. Dobson,

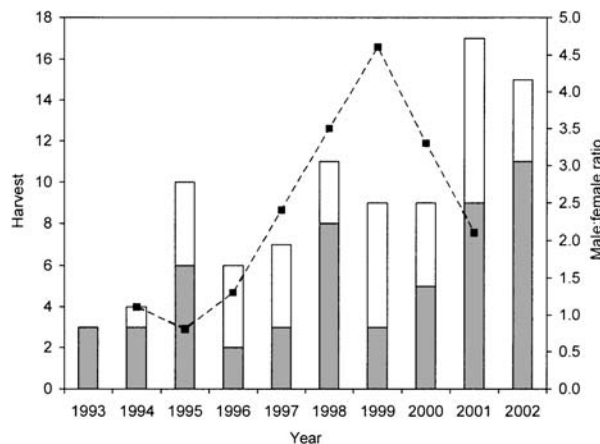


Fig. 5. Fall (filled bars) and spring (open) brown bear harvests by sport hunters in or potentially in (see text for details) the study area; dashed line indicates the 3-year running mean male:female ratio, southwestern Kuskokwim Mountains, Alaska.

Table 3. Subsistence harvest of brown bear from permit reports and interview surveys for the Western Alaska Brown Bear Management Area, Alaska, USA.

	1991		1992		1993		1994	
	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring
Permit reports ^a	–	–	4	3	4	0	1	
Interview surveys ^b	14	24	11	8	11	3	9	
Interview surveys ^{b,c}	5	4	6	1	4	0	5	

^aUnpublished data, Alaska Department of Fish and Game, Bethel, Alaska, USA.

^bFrom Andrew and Brelsford (unpublished report 1993) and Hensel (unpublished reports 1994, 1995).

^cFrom or potentially in the study area.

Fish and Wildlife Protection, Bethel, Alaska, USA, personal communication, 2002) and an additional 3 bears might have been harvested within the study area (S. Kovach, unpublished data); no bears were reported harvested by subsistence hunters during this period (P. Perry, Alaska Department of Fish and Game, Bethel, Alaska, USA, personal communication, 2003).

Population growth rate

Although data were not available to directly calculate survival between mean weaning age (2.9 yrs) and 4 years of age, we estimated it to be 86.2–90.2% by averaging mean annual survival for 1 and 2 year old offspring (72.4–83.8%, $n = 84$ bears) with that of 4–7 year olds (96.7–100%; $n = 19$ bears; Table 1); these values are similar to that reported by Case and Buckland (1998). We assumed no difference in survival between males and females <4 years old. Only one 4-year-old radiocollared bear was found to have a litter (which did not survive), so reproductive rates for the 0–4-year-old age classes was set to 0 (Table 1). We found overall reproductive rates estimated following the McLellan method significantly higher ($P < 0.001$) than those following the Eberhardt method (Table 1). Overall reproductive rates were also significantly different temporally (both methods, $P < 0.001$; Table 1). Reproductive rates were found to vary with age as well. During the first half of the study, both methods found 15–19-year olds with significantly higher reproductive rates ($P = 0.024–0.026$) than the other 3 adult age classes; there was no difference between the other 3 adult age classes. During the second half of the study, the McLellan method found reproductive rates for 10–14-year olds higher ($P = 0.021$) than 15–19 year olds, while the Eberhardt method found 10–14 year olds

Table 4. Estimated lambda (λ) between periods, reproductive rate method (McLellan, Eberhardt), and grouping method (mean, age specific; see text for details) for female brown bears in the southwestern Kuskokwim Mountains, Alaska.

Time	λ (90% confidence interval)			
	McLellan ^a		Eberhardt ^b	
	Mean	Age specific	Mean	Age specific
1993–97	1.042 (1.032–1.051)	1.047 (1.038–1.056)	1.035 (1.025–1.045)	1.039 (1.030–1.048)
1998–2002	0.970 (0.956–0.983)	0.997 (0.983–1.011)	0.963 (0.949–0.976)	0.995 (0.980–1.010)

^aMcLellan (1989a).^bEberhardt (1995).

higher ($P = 0.045$) than 20–29 year olds; both methods found no difference between the other 3 adult age classes.

Lambda differed significantly between 1993–97 and 1998–2002 ($P < 0.001$ for all mean survival and reproductive rates and age-class specific values with the McLellan method reproductive rate; $P = 0.003$ for age-class specific values with the Eberhardt method reproductive rate; Table 4). Within the 1993–97 period, λ was not different ($P = 0.5–0.6$) between reproductive rate methods and groupings (i.e., mean versus age class specific parameter values). Within the 1998–2002 period, λ was not different between reproductive rate methods, but was different ($P = 0.058–0.099$) within groupings (Table 4). Fecundity over all age classes accounted for only 6–7% of the elasticity of the λ estimate, regardless of how reproductive rate was calculated (i.e., mean or age group specific). Survival in the youngest ages (e.g., <5 years old) accounted for 32–36% of the elasticity of the λ estimates, whereas survival of 5–14 year old females accounted for 43–47% of the elasticity.

We estimated λ for 3-year periods (Fig. 6) constituting each half of the study. In the first half of the study, the negative λ during the 1995–97 period was driven by lower adult and 1- and 2-year-old offspring survival (Fig. 3) compared to 1993–95, 1994–96, and 1996–98. Negative λ for the last 4 periods (i.e., second half of the study) were largely driven by lower adult survival compared to the first half of the study. The increasing, but still negative λ during the 2000–02 period was due to increased offspring survival (Fig. 3).

Discussion

The estimated mean age of primiparity (7.2 yrs) and first weaning (9.5 yrs) reported here are among the oldest recorded for interior Alaskan studies and intermediate for coastal Alaska populations (Table 5).

However, of the relevant studies, only Key (2001) used the method of Garshelis et al. (1998), which yields an unbiased estimate of average age of primiparity. The other estimates in Table 5 used conventional methods which only consider individuals surviving to produce offspring, negatively biasing estimates of mean age of primiparity (Garshelis et al. 1998). Other reported mean ages of primiparity ranged between 5.8 and 8.7 years (McLellan 1989a, Wielgus et al. 1994, Case and Buckland 1998, Schwartz et al. 2005).

More important, we believe, is the mean age of first weaning. Several studies reporting mean age of primiparity for brown bears commented that not all first litters survived (e.g., McLellan 1989a, Miller 1990). Few reported age of first weaning, a more relevant life history parameter. In our study, the estimated unbiased mean age at first weaning was 2.3 years greater than the

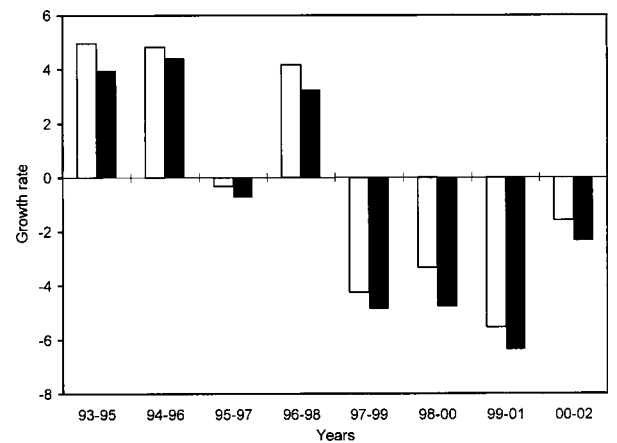


Fig. 6. Estimated lambda from mean adult survival, age-specific subadult survival (see text for details), and mean reproductive rates for female brown bears in the southwestern Kuskokwim Mountains, Alaska (open bars = reproductive rate calculated following McLellan [1989a]; filled bars = Eberhardt [1995] method).

Table 5. Reproductive parameters for interior Alaska brown bear populations.

Study area ^a	Mean age of first reproduction (yrs)	Mean age of first weaning (yrs)	Mean COY litter size	Mean litter size at weaning	Mean age at weaning (yrs)	Birthing interval (yrs)	Weaning interval (yrs)	Females produced/yr ^b	Females weaned/yr ^c
Kuskokwim Mountains	6.9	9.3	2.0	1.5	2.9	2.6	4.6	0.38	0.17
Susitna River, southcentral Alaska	nr ^d	nr	2.1	1.7	2.0	2.1	4.2	0.50	0.20
Upper Susitna River, southcentral Alaska	5.6	nr	2.1	1.9	2.2	2.1	4.1	0.50	0.23
Denali National Park	7.6 ^e	10.3 ^e	2.1	1.6	2.9	2.1	4.5	0.50	0.17
Northcentral Alaska Range	6.0	8.7	2.1	1.9	2.2	2.7	4.0	0.39	0.24
Noatak River, Northwest Alaska	6.1	nr	2.2	1.8	2.9	3.3	3.9	0.33	0.22
Eastern Brooks Range	10.1	nr	1.8	nr	nr	4.2	nr	0.21	–
Western Brooks Range	7.9	nr	2.0	1.7	nr	4.1	4.1	0.24	0.21

^aKuskokwim Mountains, this study; Susitna River, Miller (1988); Upper Susitna River, Miller (1993, 1997); Denali Nat'l Park, Keay (2001; US Geological Survey, Biological Resources Division, Gainesville, Florida, USA, personal communication, 2004); Northcentral Alaska Range, Reynolds (1997, 1999); Noatak River, Ballard et al. (1993); Eastern Brooks Range, Reynolds (1976); Western Brooks Range, Reynolds and Hechtel (1984).

^bMean COY (cubs of the year) litter size x 0.5 and dividing by the birth interval.

^cMean weaned litter size x 0.5 and dividing by the weaning interval.

^dNot reported.

^eCalculated following Garshelis et al. (1998).

unbiased mean age of primiparity. Given that our sample of females successfully weaning their first litter was 20 and that the oldest individual to wean its first litter was 14 years old, we could still be underestimating this parameter. However, similar values have been observed elsewhere in Alaska (Reynolds 1997, Keay 2001) and do not appear to be unique to our population. Managers who focus on mean age of primiparity instead of mean age of first weaning would overestimate fecundity because the true value of when females give birth to litters that are successfully weaned is potentially much higher. Absent sufficient data, the suggestion by Schwartz et al. (2003) that primiparity is a gradual process maximizing at age 8 appears warranted; yet, in our case, this would have still overestimated fecundity and total reproductive life.

Mean size of cub litters (2.0) and size of weaned litters (1.5) recorded in this study were smaller than virtually all interior Alaskan studies (Table 5) but were within the range reported for coastal populations found in southeast Alaska, Kodiak Island, McNeil River, and the Alaska Peninsula (Schoen and Beier 1990, Smith and Van Daele 1991, Sellers and Aumiller 1994, Miller et al. 2003). These coastal populations have higher bear densities, longer growing seasons, and access to greater forage resources than our study area.

Direct comparisons of reproductive intervals across studies are difficult due to subtle differences in definitions of a reproductive interval. Acknowledging

these differences, our population had one of the highest production of offspring, yet the lowest number of female offspring weaned/year in Alaska (Table 5). The rate of 0.17 female offspring weaned/adult female/year was also lower than that reported for both southeast Alaska and Kodiak (Schoen and Beier 1990, Smith and Van Daele 1991), and Yellowstone National Park (0.63 offspring weaned/yr; Craighead et al. 1974). Measuring productivity independent of mortality (0.38 female cubs/adult female/yr; Table 5) shows that the Kuskokwim Mountains were slightly more productive than Yellowstone (0.31–0.32; Schwartz et al. 2005) and the Selkirk Mountains (0.37; Wielgus et al. 1994), and slightly less than the central Canadian Arctic (0.40; McLoughlin et al. 2003) and southeast British Columbia (0.44; McLellan 1989b). These findings are interesting considering our population had access to spawning salmon (*Oncorhynchus* spp., Collins et al. 2005), whereas little, if any, salmon were available in these other study areas.

Although the age-specific pattern of reproduction did not match Model D of Schwartz et al. (2003:115), the pattern of per capita production did follow their distribution of data points. All females ≥ 20 years old were reproductively active until their deaths or removal of their radiocollars. As Fig. 2a indicates, this oldest age group had reduced production of offspring following the general pattern suggested by Schwartz et al. (2003); however, reproductive senescence (i.e., cessation of reproductive activity) was not observed here, in contrast

to other populations (e.g., Craighead et al. 1974, Wielgus et al. 1994, Miller 1997).

Annual adult female survival (91.0–97.2%) was within the ranges found elsewhere in Alaska (Smith and Van Daele 1991, Reynolds 1997, Schwartz et al. 1999, Sellers and Miller 1999, Keay 2001). Studies outside Alaska reported mean annual adult female survival rates of 92.6–96.0% (McLellan 1989b, Wielgus et al. 1994, Case and Buckland 1998, McLellan et al. 1999, Schwartz et al. 2005).

Similar to McLaughlin et al. (1994) and Schwartz et al. (2005), increasing female age resulted in higher rates of offspring survival. Survival of dependent offspring (Table 1) was generally lower than in coastal (Smith and Van Daele 1991, Sellers and Aumiller 1994, Sellers and Miller 1999) and interior Alaska populations (Miller 1988, 1997; Reynolds 1997). Only Denali (Keay 2001) and Katmai National Parks (Sellers and Miller 1999) had lower survival rates. Other brown bear populations outside Alaska exhibited higher dependent offspring survival rates, ranging between 64% and 94% (Knight and Eberhardt 1984, McLellan 1989b, Wielgus et al. 1994, Case and Buckland 1998, Schwartz et al. 2005). Cannibalism by adult males has been suspected as a major mortality source for dependent offspring in brown bear populations across Alaska (Troyer and Hensel 1962, Glenn et al. 1976, Reynolds 1980, Reynolds and Hechtel 1982, Miller 1984, Dean et al. 1986). The high rate of cub loss during May and June (54% of all cub losses) is similar to that recorded in Denali National Park and the Susitna study areas of Miller et al. (2003), but was intermediate for values reported from the Alaska Peninsula (Miller et al. 2003). This pattern of early cub loss was opposite that reported by Schwartz et al. (2005).

Illegal harvests of brown bears were known to have occurred in the general region. Members of the Western Alaska Brown Bear Management Area Working Group expressed concern over increasing illegal harvests of brown and black bears (*U. americanus*) in southwest Alaska, particularly near villages (Van Daele et al. 2001, Kovach et al. unpublished report 2003). Alaska Fish and Wildlife Protection officers reported a number of complaints, and investigations occurred in the southwestern Kuskokwim Mountains between 1993 and 2003 (J. Pagel, Fish and Wildlife Protection, Aniak, Alaska, USA, personal communication, 2003; C. Yoder, Fish and Wildlife Protection [retired], Bethel, Alaska, USA, personal communication, 2001) but could not estimate the number of illegal harvests. A radiocollared female was harvested in September 2002 but was never reported by

sport or subsistence hunters. Further, no DLP takings were reported within or near the study area (Alaska Department of Fish and Game, unpublished data).

Lacking an estimate of illegal harvest, the sum of the reported sport and estimated subsistence harvest is therefore a minimum value of total mortality. In general, we observed an increasing trend in sport harvest (Fig. 5); however, the mean reported sport harvest more than doubled during the last 2 years of the study (2001 and 2002). In contrast, subsistence harvest appeared to decline over time (Table 3). Subsistence harvests have a history of oscillations with significant spikes, particularly in the spring (Coffing and Pete 1992; T. Brelsford, Bureau of Land Management, Anchorage, Alaska, USA, personal communication, 1993–98; M. Coffing, Alaska Department of Fish and Game [retired], Bethel, Alaska, USA, personal communication, 1997, 2002); such a spike may explain the 1992 harvest (Table 3). Reporting rate from the registration permits has been slightly lower, but reasonably consistent, since 1994 (R. Seavoy, Alaska Department of Fish and Game, Bethel, Alaska, USA, personal communication, 2004), indicating that at least the 1993–94 harvest rate of 5.0 bears/year may be a valid estimate. Using the 2.5:1 male:female ratio from Andrew and Brelsford (unpublished report 1993) and Hensel (unpublished reports 1994, 1995), applied to a 5 bear/year average harvest (1994 harvest, Table 3) would result in 3.5 males and 1.4 females harvested annually by subsistence hunters. Combining the overall mean sport harvest rate with the estimated subsistence harvest yields a total annual harvest during 1993–97 of 7.3 males and 5.2 females, and 12.1 males and 4.8 females during 1998–2002.

Van Daele et al. (2001) presented a minimum density estimate (18.2 independent bears/1,000 km²) for this study area, which we were unable to refine. Their estimate yields a minimum population of 126 independent bears, 60% of which were females, for our study area. Using our estimate of annual harvest, approximately 9.1% of the minimum population (5.5% of the females) were harvested annually during 1993–97 and 13.4% (6.3% of the females) during 1998–2002. Populations with higher offspring survival than the Kuskokwim Mountains (Table 5) which recorded female harvest rates of 6.4% and 16.7% (Miller 1997, Reynolds 1997) reported population declines.

The timing of our cub losses suggests that infanticide could affect cub survival in southwest Alaska. Both Swenson et al. (2001) and Wielgus et al. (2001) suggested that removal of resident adult males negatively affect cub survival. Such effects were manifested

through reduced survival in subadult age classes and decreased reproductive rates. Although reported sport harvest increased throughout our study (particularly in the last 2 years; Fig. 5), survival across all age classes may have increased toward the end of the study (Fig. 3); overlapping confidence intervals makes this assessment uncertain, however. Additionally, our reproductive rate, as calculated following Wielgus et al. (2001), increased in the second half of our study (1993–97, 0.72 cubs/yr; 1998–2002, 0.81 cubs/yr). Both of these findings are contrary to Swenson et al. (2001) and Wielgus et al. (2001). Compared to the first half of the study, we observed a decrease in cub survival and an increase in the loss of whole cub litters during the second half of the study. Whole litter loss has been observed to be higher in low to moderate density populations that are heavily hunted (Swenson et al. 2001, Miller et al. 2003).

During the first half of our study, the estimated λ suggested that the population grew at 3.5–4.1% (using mean survival and reproductive rates). However, when survival and reproductive rates were broken into age classes, the estimated λ suggested the population grew at 3.9–4.7%, which was not significantly different from the previous method. During the second half of the study, using mean reproductive and survival values, the estimated λ indicated the population declined at 3.0–3.7%; using age-class specific parameter values, estimated λ was higher (0.993–0.997) but still indicated a declining population. Unlike Schwartz et al. (2005), we had a significant difference between reproduction rates using the McLellan and Eberhardt methods. Along with significant temporal differences in reproductive rates, we found some differences between age classes (Table 1). Like Schwartz et al. (2005), elasticity analysis showed that fecundity was a minor contributor (6–7%) to the λ estimate. For both halves of our study, elasticity analysis of λ reflected the influence of survival of dependent offspring as well as 5–14-year olds.

Conclusions

We believe age of first weaning to be a more important parameter than age of primiparity and encourage other researchers to calculate and report it. Without it, managers should seriously consider the suggestion by Schwartz et al. (2003) that primiparity is a gradual process.

We agree with the conclusion by Van Daele et al. (2001) that there was no apparent increase in subsistence harvest as a result of liberalized regulations. However, we acknowledge that the sex ratio of the harvest may

have changed since the early 1990s. The population was capable of withstanding the mean annual harvest at the time the study was initiated. However, harvest appeared to be at or beyond a sustainable rate at the conclusion of the study. Changes in offspring survival and reproduction recorded in southwest Alaska are not fully explained by sexually-selected infanticide (e.g., Swenson et al. 2001, Wielgus et al. 2001) and need further investigation. Our analysis of λ concurs with Eberhardt (1990) in that adult female survival rates >90% are needed to sustain this population.

We found differences between age groups for both survival and reproductive rates. In the first half of the study the difference in the λ estimates were insignificant. In the second half of the study, while indicating a declining population, the λ estimated with the age-class specific parameters was significantly higher than that estimated with mean values. We are unsure how much of the difference was due to sampling variance and process variance, but encourage others to evaluate differences between age-class specific and mean parameter values.

Elasticity analysis indicated that managers in southwest Alaska need to be wary of the harvest of females <15 years old. Because only basic harvest data are obtained from subsistence hunters, sex and age structure is largely unknown for up to 45% of the estimated harvest. Such uncertainty limits manager's ability to effectively manage the brown bear harvest in southwest Alaska, and methods for collecting more complete harvest data should be considered. Further, that subsistence hunters historically had spikes in their harvest needs to be considered in management. Managers of the YDNWR, TNWR, and nearby Bureau of Land Management lands are required to manage wildlife populations for subsistence harvest opportunities under Public Law 96-487. We agree with recommendations of Eberhardt (1990) and Garshelis (2002) that, given uncertainty in parameters, whether those parameters are characteristics of the population or a result of habitat, should be reason enough to err on the side of caution when considering management options.

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Literature cited

- AKÇAKAYA, H.R., M.A. BURGMAN, AND L.R. GINZBURG. 1999. Applied population ecology: principles and computer exercises using RAMAS EcoLab. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- AMSTRUP, S.C., AND G. DURNER. 1995. Survival rates of radio-collared female polar bears and their dependent young. *Canadian Journal of Zoology* 73:1312–1322.
- BALLARD, W.B., L.A. AYRES, D.J. REED, S.G. FANCY, AND K.E. RONEY. 1993. Demography of grizzly bears in relation to hunting and mining development in northwestern Alaska. Scientific Monograph NPS/NRARO/NRSM-93/23.
- CASE, R.L., AND L. BUCKLAND. 1998. Reproductive characteristics of grizzly bears in the Kugluktuk area, Northwest Territories, Canada. *Ursus* 10:41–47.
- CASWELL, H. 1989. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.
- COFFING, M., AND M. PETE. 1992. Subsistence use of brown bear in western Alaska—a report to Alaska Board of Game. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- COLLINS, G.H., S.D. KOVACH, AND M.T. HINKES. 2005. Home range and movements of female brown bears in southwestern Alaska. *Ursus* 16:181–189.
- CRAIGHEAD, J.J., J.R. VARNEY, AND F.C. CRAIGHEAD, JR. 1974. A population analysis of the Yellowstone grizzly bears. Montana Forest and Conservation Experiment Station Bulletin 40. Missoula, Montana, USA.
- , J.S. SUMNER, AND J.A. MITCHELL. 1995. The grizzly bears of Yellowstone. Island Press, Washington D.C., USA.
- DEAN, F.C., L.M. DARLING, AND A.G. LIERHAUS. 1986. Observations of intraspecific killing by brown bears, *Ursus arctos*. *Canadian Field-Naturalist* 100:208–211.
- EBERHARDT, L.L. 1990. Survival rates required to sustain bear populations. *Journal of Wildlife Management* 54:587–590.
- , B.M. BLANCHARD, AND R.R. KNIGHT. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. *Canadian Journal of Zoology*. 72:360–363.
- . 1995. Population trend estimates from reproductive and survival data. Pages 13–19 in R.R. Knight and B.M. Blanchard. Yellowstone grizzly bear investigations: annual report of the Interagency Study Team, 1994. National Biological Survey, Bozeman, Montana, USA.
- GARSHELIS, D.L., K.V. NOYCE, AND P.L. COY. 1998. Calculating average age of first reproduction free of the biases prevalent in bear studies. *Ursus* 10:437–447.
- . 2002. Misconceptions, ironies, and uncertainties regarding trends in bear populations. *Ursus* 13:321–334.
- GILBERT, J.R., AND M.S. UDEVITZ. 1997. Adaptation of a stage-projection model for species with multiple year reproductive cycles. *Ecological Modelling* 97:47–57.
- GLENN, L.P., J.W. LENTFER, J.B. FARO, AND L.H. MILLER. 1976. Reproductive biology of female brown bears, *Ursus arctos*, McNeil River, Alaska. *International Conference of Bear Research and Management* 3:381–390.
- HARTIGAN, J.A. 1975. Clustering algorithms. John Wiley and Sons, Inc., New York, New York, USA.
- HOOD, G.M. 2004. PopTools version 2.6.2. CSIRO Sustainable Ecosystems, Gungahlin Homestead, Canberra, Australia. <http://www.cse.csiro.au/poptools>, accessed 15 March 2004.
- KEAY, J.A. 2001. Grizzly bear population ecology and monitoring Denali National Park and Preserve, Alaska. Report of project development and findings. US Geological Survey, Alaska Biological Science Center, Anchorage, Alaska, USA.
- KNIGHT, R.R., AND L.L. EBERHARDT. 1984. Projected future abundance of the Yellowstone grizzly bear. *Journal of Wildlife Management* 48:1434–1438.
- LESLIE, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183–212.
- MATSON, G., L. VAN DAELE, E. GOODWIN, L. AUMILLER, H. REYNOLDS, AND H. HRISTENKO. 1993. A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth. Alaska Department of Fish and Game, Anchorage, Alaska, USA and Matson's Laboratory, Milltown, Montana, USA.
- MCLAUGHLIN, C.R., G.J. MANTA, JR., AND R.J. O'CONNOR. 1994. Synchronous reproduction by Maine black bears. *Ursus* 9(1):471–479.
- MCLELLAN, B.N. 1989a. Dynamics of a grizzly bear population during a period of industrial resource extraction.

- III. Natality and rate of increase. *Canadian Journal of Zoology* 67:1865–1868.
- . 1989b. Dynamics of a grizzly bear population during a period of industrial resource extraction. II. Mortality rates and causes of death. *Canadian Journal of Zoology* 67:1861–1864.
- , F.W. HOVEY, R.D. MACE, J.G. WOODS, D.W. CARNEY, J.L. GIBEAU, W.L. WAKKINEN, AND W.F. 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, P.D., M.K. TAYLOR, H.D. CLUFF, R.J. GAU, R. MULDER, R.L. CASE, S. BOUTIN, AND F. MESSIER. 2003. Demography of barren-ground grizzly bears. *Canadian Journal of Zoology* 81:294–301.
- MILLER, S.D. 1984. Big game studies. Volume VI. Black bear and brown bear. Susitna Hydroelectric Project, 1983 Annual Report. Alaska Department of Fish and Game, Anchorage, Alaska, USA.
- . 1988. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's management unit 13. Federal Aid in Wildlife Restoration Research Final Report on Project W-23-1 Job 4.21. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- . 1990. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Federal Aid in Wildlife Restoration Research Final Report on Project W-23-3, Study 4.21. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- . 1993. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Federal Aid in Wildlife Restoration Research Final Report on Projects W-22-6, W-23-1, W-23-2, W-23-3, W-23-4, and W-23-5, Study 4.21. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- . 1997. Impacts of heavy hunting pressure on the density and demographics of brown bear populations in southcentral Alaska. Federal Aid in Wildlife Restoration Research Final Report on Grants W-24-2, W-24-3, and W-24-4, Study 4.26. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- , R.A. SELLERS, AND J.A. KEAY. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus* 14:130–152.
- MUNDY, K.R.D., AND W.A. FULLER. 1964. Age determination in the grizzly bear. *Journal of Wildlife Management* 28:863–866.
- POLLOCK, K.H., S.R. WINTERSTEIN, AND P.D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- REYNOLDS, H.V. 1976. North slope grizzly bear studies. Federal Aid in Wildlife Restoration, Research Final Report on Projects W-17-6 and W-17-7, Jobs 4.8R, 4.9R, 4.10R and 4.11R. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- . 1980. North slope grizzly bear studies. Federal Aid in Wildlife Restoration. Research Progress Report on Project W-17-11, Studies 4.14 and 4.15R. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- , AND J.L. HECHTEL. 1982. North slope grizzly bear studies. Federal Aid in Wildlife Restoration Progress Report on Project W-21-2. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- , AND ———. 1983. Population structure, reproductive biology, and movement patterns of grizzly bears in the northcentral Alaska Range. Federal Aid in Wildlife Restoration Progress Report on Project W-22-2. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- , AND ———. 1984. Structure, status, reproductive biology, movement, distribution, and habitat utilization of a grizzly bear population. Federal Aid in Wildlife Restoration Final Report on Project W-21-1, W-21-2, W-22-1, and W-22-2, Job 4.14R. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- . 1997. Effects of harvest on grizzly bear population dynamics in the northcentral Alaska Range. Federal Aid in Wildlife Restoration Final Report on Grants W-24-1, W-24-2, W-24-3, and W-24-4, Study 4.25. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- . 1999. Effects of harvest on grizzly bear population dynamics in the northcentral Alaska Range. Federal Aid in Wildlife Restoration Final Report on Grants W-24-5 and W-27-1, Study 4.28. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- SCHOEN, J., AND L.V. BEIER. 1990. Brown bear habitat preferences and brown bear logging and mining relationships in southeast Alaska. Federal Aid in Wildlife Restoration Final Report on Projects W-22-1, W-22-2, W-22-3, W-22-4, W-22-5, W-22-6, W-23-1, W-23-2, and W-23-3, Study 4.17. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- SCHWARTZ, C.C., AND A.W. FRANZMANN. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. *Wildlife Monographs* 113.
- , S.M. ARTHUR, AND G.G. DEL FRATE. 1999. Cumulative effects model verification, sustained yield estimation, and population viability management of the Kenai Peninsula, Alaska brown bear. Federal Aid in Wildlife Restoration Research Progress Report on Grant W-27-1, Study 4.27. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- , K.A. KEATING, H.V. REYNOLDS, III, V.G. BARNES, JR., R.A. SELLERS, J.E. SWENSON, S.D. MILLER, B.N. McLELLAN, J. KEAY, R. McCANN, M. GIBEAU, W.F. WAKKINEN, R.D. MACE, W. KASWORM, R. SMITH, AND S. HERRERO. 2003. Reproductive maturation and senescence in the female brown bear. *Ursus* 14:109–119.

- , M.A. HAROLDSON, G.C. WHITE, R.B. HARRIS, S. CHERRY, K.A. KEATING, D. MOODY, AND C. SERVHEEN. 2005. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161.
- SELLERS, R.A., AND L.D. AUMILLER. 1994. Brown bear population characteristics at McNeil River, Alaska. *Ursus* 9(1):283–293.
- , AND S.D. MILLER. 1999. Population dynamics of brown bears after the Exxon Valdez oil spill. *Ursus* 11:73–78.
- SMITH, R.B., AND L.J. VAN DAELE. 1991. Terror Lake hydroelectric project. Final report on brown bear studies (1982–1986). Alaska Department of Fish and Game, Kodiak, Alaska, USA.
- SPSS. 1999. SYSTAT 9, Statistics 1. SPSS Inc., Chicago, Illinois, USA.
- SWENSON, J.E., F. SANDEGREN, S. BRUNBERG, AND P. SEGERSTRÖM. 2001. Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12:69–80.
- TROYER, W.A., AND R.J. HENSEL. 1962. Cannibalism in brown bears. *Animal Behavior* 10:231.
- VAN DAELE, L.J., J.R. MORGART, M.T. HINKES, S.D. KOVACH, J.W. DENTON, AND R.H. KACYON. 2001. Grizzlies, Eskimos and biologists: cross-cultural bear management in southwest Alaska. *Ursus* 12:141–152.
- WIELGUS, R.B., W.L. WAKKINEN, AND P.E. ZAGER. 1994. Population dynamics of Selkirk Mountain grizzly bears. *Journal of Wildlife Management* 58:266–272.
- , F. SARRAZIN, R. FERRIERE, AND J. COLBERT. 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation* 98:293–303.

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