BROWN BEAR POPULATION CHARACTERISTICS AT MCNEIL RIVER, ALASKA

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Abstract: Observations of recognizable brown bears (*Ursus arctos*) at McNeil River State Game Sanctuary (MRSGS) during 1963-91 provided long-term data on population size, sex and age composition, reproductive success, and survival rates. Bears using MRSGS increased from 66 (SE = 5.8) during 1969-84 to 113 (SE = 8.5) during 1987-91. Adult sex ratio averaged 121 males/100 females. This reflected a low exploitation rate and greater seasonal movements of male bears. Adult survival rates averaged 0.94 for males and 0.93 for females. Since 1963, 31% of 168 cubs disappeared between 0.5 and 1.5 years of age. Kaplan-Meier estimates of summer survival rates were 0.67 for cubs and 0.89 for yearlings. Twenty females, observed for a total of 242 bear-years, raised 83 yearlings in 47 litters. Lifetime recruitment for 11 females observed from sexual maturity to presumed death averaged 2 (range 0-8) yearlings. Despite the high ratio of adult males to females and increased population size, we did not detect a density-dependent suppression of cub production or survival.

Brown bears are a K-selected species (Cowan et al. 1974). Absent substantial human-induced mortality, populations should stabilize at carrying capacity and be regulated by density-dependent mechanisms, including one or more of the following: lower reproductive rates, lower survival rates, and higher dispersal rates. Bunnell and Tait (1981) suggested that reproductive rates for bears are influenced primarily by nutrition and are largely density independent. They further suggested that mortality factors, including dispersal, were most likely to regulate populations. Their evaluations and most studies have focused on bear populations subjected to significant human-caused mortality where intrinsic population dynamics may be obscured.

Continuing debate over grizzly bear population dynamics in Yellowstone National Park (Mattson and Reid 1991, McLellan 1994) illustrates the need for long-term study of bear populations, especially where human influences are minimal. Within the contiguous 48 states and Canadian provinces, no single jurisdictional land holding is large enough to provide the level of protection necessary to allow natural regulatory mechanisms to play a dominant role in population dynamics (Pearson 1975, Martinka 1982, McLellan 1989). Even within Alaska, only a few brown bear populations under study (e.g., Denali National Park and MRSGS-Katmai National Park [Katmai NP]) are influenced primarily by natural factors.

Recent studies using radio transmitters have greatly increased knowledge of brown bear reproductive and survival rates and other population parameters for several Alaskan bear populations subject to significant impacts from humans (Miller 1987, Schoen and Beier 1990, Ballard et al. 1991, Smith and VanDaele 1991, and Reynolds 1993). Only a few studies have been able to follow individual bears for more than 2 reproductive cycles.

Long-term study of individual-life histories has been possible at McNeil River because of the presence of habituated, individually recognizable bears that visit the site to catch salmon during mid-summer. In this paper, we build upon earlier data collected at this site and compare contemporary values with earlier results (Glenn et al. 1976, Modafferi 1984). We continued monitoring recognizable bears, as well as total numbers and composition; these data allow estimation of reproductive and survival rates. This study eventually will be combined with a separate study in adjacent Katmai NP to further test the hypothesis that population regulatory mechanisms differ between these high density, protected populations and moderately harvested, lower density populations elsewhere in southwestern Alaska.

STUDY AREA

The MRSGS (Fig. 1) is approximately 340 km southwest of Anchorage on Kamishak Bay at the base of the Alaska Peninsula. The area was described by Faro and Eide (1974), Glenn et al. (1976), Egbert (1978), Bledsoe (1987), and Aumiller and Matt (1994). The McNeil River drainage was closed to bear hunting in 1955 and in 1967 was legislatively designated a state sanctuary encompassing about 340 km². A presidential proclamation in 1978 and subsequent legislation
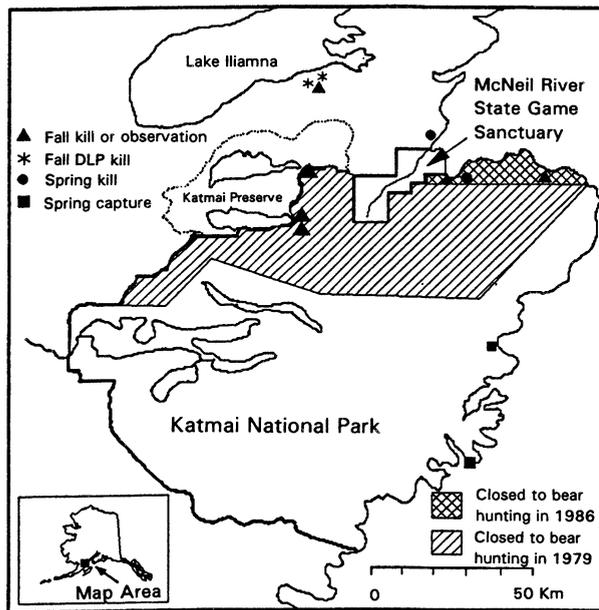
Fig. 1. Locations of McNeil River State Game Sanctuary and McNeil River bears seen or killed outside the sanctuary.

expanded Katmai NP (formally a national monument). In 1986 the state Board of Game closed bear hunting on an additional 300 km² of state land between MRSGS and Katmai NP, putting MRSGS on the northern edge of an area of about 15,600 km² closed to bear hunting (Fig. 1).

Brown bears are attracted to the sanctuary in June to feed on a small intertidal sedge (*Carex lyngbyaei*) meadow and an early run of red salmon (*Oncorhynchus nerka*) in Mikfik Creek. Bear numbers build during June and the first half of July and peak the last 2 weeks of July when chum salmon (*O. keta*) are available at McNeil Falls, a short stretch of rapids that impedes the migration of salmon 1.8 km upstream from salt water. By mid-August bear numbers decline by up to 80% as bears move to other river systems or begin foraging for berries.

METHODS

The observation period at MRSGS varied within the dates of 23 May to 19 September and most consistently covered June through August. Daily observations typically occurred from mid-morning to early evening. Bears were identified and catalogued based on sex, estimated age, and distinguishing characteristics, including both physical and behavioral traits. Where age was not known, experienced observers, including

Aumiller from 1976 to 1991, classified bears as subadults (bears estimated <5) or adults. Survival rates were calculated only for recognizable adults and for offspring of such bears. Cub survival was measured by comparing average litter sizes for cubs (refers to bears <1 year old) and yearling litters, by documenting the disappearance of offspring of known females between their first and second summers, and by calculating summer survival rates for cubs and yearlings using the Kaplan-Meier technique (Pollock et al. 1989). For this last approach, offspring were censored once the family left the study area.

Salmon escapements were estimated primarily from aerial surveys conducted by fisheries biologists from the Commercial Fisheries Division of ADF&G. These surveys provide an index to salmon abundance between years.

Spearman's coefficient of rank correlation was used to test the hypothesis of density dependent regulation of recruitment. Means were compared using t test.

RESULTS AND DISCUSSION

Population Size and Density

Enumeration and classification of bears using MRSGS has improved in the 37 years since McNeil was first publicized. Early accounts of bears seen at McNeil Falls provide a useful historical baseline to our data. Rhodes (1954) counted 32 bears in one day. I. Marx, a stream guard stationed at McNeil from 6 May to 10 August 1958, accounted for at least 115 different bears during the course of the summer and saw 58 at once (I. Marx, field notes 1958). The reliability of Marx's observations is unknown, but details were presented comparing an independent morning aerial count of 53 bears with a minimum of 87 different bears seen from the ground that day by Marx (Rausch 1958). In 1991, 7 morning aerial surveys of McNeil River and McNeil Lagoon between 15 July and 4 August tallied an average of 58% of the bears cataloged from ground counts during the same days (ADF&G, unpubl. data). Based on the 1991 comparisons and results of other studies comparing aerial counts with ground observations (Erickson and Siniff 1963, V.G. Barnes, U.S. Fish and Wildl. Serv., Kodiak, Alaska, pers. commun.), Marx's tally of 64% more bears than seen during the aerial survey seems plausible. From 1963 to 1967 the total number of bears observed during the peak of bear activity was estimated at 30-35 (ADF&G, unpubl. data), and the highest number of different bears recognized in one day was 13 in 1967. In 1968 a

minimum of 30 independent bears and 18 offspring was recorded.

There are several possible reasons for the apparent decline in bear use from 1958 through the 1960s. During the 1960s, biologists were generally present for less than a month and concentrated their efforts on capturing bears. Consequently they did not devote full attention to identifying unmarked bears, and their counts were conservative. In addition, the effects of ground capture operations, from both disturbance and capture mortalities, along with increasing and unregulated public visitation, may have artificially reduced the number of bears using the sanctuary.

Improved data collection began in 1969 with the arrival of a series of graduate students from Utah State University. During 1969-84, the total number of bears cataloged at MRSGS was stable, averaging 66 bears (range 56-77, SE = 5.8) per year (Table 1). The total population and number of independent bears increased at rates of 10.3% and 6.4% per year, respectively, from 1983 to 1989, and then declined slightly (Table 1). During 1987-91 an annual mean of 113 bears (range 106-126, SE = 8.5) were present. Numbers of adults of both sexes and dependent offspring increased while the number of subadults remained stable (Table 1).

The only other documented case of brown bear population growth in Alaska was at Black Lake on the Alaskan Peninsula where during 1974-85 the population recovered from excessive harvests. Stream survey counts of bears at Black Lake indicated growth rates of 6-7% and 9-10% for total bears and independent bears, respectively (Miller and Sellers 1990). Hunting seasons were restricted during the recovery period, and undoubtedly, survival rates for males and single females increased as a result, thus explaining why the rate of increase was higher for independent bears than for the whole population. At MRSGS, in contrast, the whole population grew faster than the independent cohort, primarily because the number of subadults did not increase, presumably because of dispersal or higher mortality.

Several factors may have been involved in the increase in bear numbers seen at MRSGS since the early 1980s. Katmai National Monument (changed to Katmai NP by Congress in 1980) was expanded in December 1978 by presidential proclamation to encompass about 4,000 km² just south and west of MRSGS. Three of the 8 bears marked at MRSGS that were later killed by hunters came from this area (Fig. 1). In 1986 the Alaska Board of Game closed bear hunting in about 300 km² of state land between MRSGS

and Katmai NP. Three other marked McNeil bears were killed by hunters in this area. Thus by 1986, expansion of Katmai NP and the state closure protected bears in an area where 75% of the previous known harvest of McNeil bears had occurred. The area north and northwest of the sanctuary remains open to bear hunting on an alternating season schedule, i.e., since 1975 hunts occurred in October of odd years and May of even years. Harvest rates were considered moderate and probably ranged from 2 to 5% annually during the course of this study, but were probably lower for the subpopulation of bears using MRSGS because only a portion of these bears used areas open to bear hunting. Nevertheless, there is evidence to suggest that even the low level of exploitation exerted upon bears using MRSGS had a dampening effect on population growth. From 1975 to 1991 there was no growth for independent bears after years with sequential fall and spring hunts (r = -0.01) compared to a 0.10 rate of increase for years when the season was closed (t = 1.91, df = 14, P < 0.05).

Another factor contributing to the increase in bears using MRSGS may have been management practices at the sanctuary, including strict control of the number and activities of visitors (Aumiller and Matt 1994). Beyond what was occurring at MRSGS, the trend of increasing bear populations was regional and not just a local phenomenon (Miller and Sellers 1990). Salmon runs through the region were very strong in the 1980s and weather conditions were mild. These favorable environmental conditions may have increased productivity and survival, but specific documentation is not available.

Density.—McNeil River State Game Sanctuary has gained fame because of the unique concentration of bears assembled in mid-summer. During the peak of the chum salmon run, the density within the core 10 km² around the falls was >11 bears/km². On several days over 100 individual bears were recorded in this core area, and it is highly probable that several other less habituated and uncatalogued bears fished at McNeil Falls during times when people were not present. Peak site-specific density was recorded at 120 bears/km² when 66 bears were in view at once from the observation pad in an area of approximately 0.55 km².

The geographic area from which bears are attracted to MRSGS is not fully measured. Kill locations and several visual observations of bears marked at MRSGS were widely dispersed (Fig. 1). In 1973 an adult female was killed in a defense of property incident about 48 km northwest of McNeil Falls. Two adult males, both long-time users of MRSGS, appeared at

Table 1. Brown bear population size and composition at McNeil River, Alaska, 1969-91.

Year	Dependent offspring		Maternal females		Single adult females	Adult males	Adults unknown sex	Subadults			Total
	Cubs	Older offspring	No. with cubs	No. with older offspring				Females	Males	Unkn. sex	
1969	3	30	1	14	6	6	12				72
1970	3	20	2	8	9	9	14				65
1971	14	6	9	3	11	14	6			13	76
1972	9	9	3	5	14	18	4			3	66
1973	6	3	3	2	15	21	5			11	66
1974	13	3	5	2	4	19	1	5	3	1	56
1975	3	20	2	8	9	9	14				65
1976	7	13	3	6	5	16	1	4	0	3	58
1977	8	13	3	7	8	18	0	3	5	4	69
1978	10	10	4	4	6	18	0	4	4	5	65
1979	8	9	4	5	8	19	0	2	0	3	58
1980	10	2	5	1	8	23	1	6	0	4	60
1981	4	10	3	5	10	26	0	9	1	5	73
1982	9	7	4	3	9	20	0	11	1	3	67
1983	2	10	2	5	15	22	0	9	4	1	70
1984	12	5	6	3	16	22	0	8	5	0	77
1985	13	15	7	9	12	27	0	2	10	0	95
1986	13	13	6	8	11	31	0	7	7	0	96
1987	16	14	7	7	13	34	0	7	8	0	106
1988	19	12	7	7	13	34	0	9	8	0	109
1989	15	27	6	13	14	42	0	4	5	0	126
1990	13	21	6	10	16	37	0	5	5	0	113
1991	21	9	10	5	12	41	0	6	4	0	108

McNeil Falls in July 1989 with ear tags applied 2 months earlier 75 km and 114 km south on the coast of Katmai NP.

The density at McNeil Falls at peak use, while intriguing, is not reflective of average annual density and consequently is not a good measure of regional habitat quality. In 9 of 10 areas throughout Alaska where the brown bear density was measured, the capture-recapture census technique was applied in spring when bear distribution is usually more dispersed (ADF&G unpubl. data). The study areas closest to MRSGS where densities have been measured were the coast of Katmai NP (R.A. Sellers and S.D. Miller unpubl. data), 2 areas on Kodiak Island (Barnes et al. 1988), and Black Lake (Miller and Sellers 1990). Densities in these areas ranged from 191 to 550

bears/1,000 km^2. We believe that the spring density in MRSGS is near the mid-point of this range.

Population Composition

The extent to which bears cataloged at MRSGS represent a cross section of the regional bear population is not fully known. The extreme concentration of bears at McNeil Falls and the extended period during which bears were cataloged might have affected the composition of bears. Male bears have larger home ranges and consequently are more likely to discover and use sites with concentrated food resources. This potential bias is exacerbated if observations are made over a prolonged period (Miller 1990a). Furthermore, females with litters or subadults may avoid McNeil Falls because of intraspecific strife. Since 1963, 4

recognizable adult females were absent a total of 5 years when they had cub litters, but brought their yearlings to McNeil Falls the following year. Two of these females only had 1 litter. The other 2 females brought 9 of 12 cub litters to McNeil Falls, but did not appear with the other 3 litters until they were yearlings. Twenty-five other recognizable females brought all their cub litters (n = 55) to McNeil Falls. Thus the rate of avoidance for females with cub litters was 7%. No recognizable females were known to have been absent when they had yearling litters. Some subadults may also have avoided McNeil Falls, but we were unable to document temporary "absenteeism" because few subadults were recognizable between years. It was apparent that most subadults that used MRSGS were relegated to peripheral areas or used prime fishing spots only when more dominant bears were not present (Egbert 1978). The rate of avoidance by nonhabituated bears is also unmeasured, but we believe stricter control of visitor numbers and activity exerted after 1973 led to greater habituation and less avoidance (Aumiller and Matt 1994). While we recognize that avoidance of McNeil Falls by any particular class of bears would bias composition data, we believe the bias to be relatively small.

Bears frequenting the MRSGS have been classified by sex, age, and family status since 1969 (Table 1); however, the relatively large number of single bears of undetermined sex prior to 1976 limits calculation of sex ratios to 1976-91. The adult sex ratio was 121 males/100 females (range 88-164, SE = 20.5). Miller (1990a) reported that the adult sex ratio in a southcentral Alaska study area declined from 113 to 38 males/100 females as exploitation increased during 1979-87. At Black Lake on the Alaska Peninsula, the adult sex ratio increased from 17 to 39 males/100 females from 1972 to 1989 as the population recovered from excessive harvests (Miller and Sellers 1990). On the central coast of Katmai NP the adult sex ratio was 76 males/100 females in 1989-90 (R. A. Sellers, Alaska Dep. of Fish and Game, unpubl. data). Based on the trend that higher exploitation rates result in lower male/female ratios, we conclude that the McNeil population is experiencing light hunting pressure.

Population composition data collected during aerial surveys, where distinction between sexes are unreliable, are sometimes expressed as the percent of the population not in family groups (hereafter referred to as "single" bears). An average of 71% of bears (n = 449) seen on 9 repetitive aerial surveys of McNeil River during 15-19 July 1991 were single (S. Miller, Alas. Dep. of Fish and Game, Anchorage, pers.

commun.). This compares to an average of 73% single bears seen from the ground on these same days. Since 1976 single bears have made up 61% (range 52-73%, SE = 6.5) of the McNeil population. Hunting regulations protect cubs, yearlings, and their mothers. Thus in intensely hunted populations the proportion of single bears is reduced; and, as with sex ratios, the proportion of single bears may provide a crude index to the rate of exploitation. The bear population along the central coast of Katmai NP may be the most protected population of brown bears in North America. In 1989, 65% of 1,013 bears seen during aerial surveys were single (R. A. Sellers, Alaska Dep. of Fish and Game, unpubl. data). On the other extreme, when harvest pressure was very high on the Alaska Peninsula in the late 1960s and early 1970s, less than 20% of the bears seen on stream surveys were singles (Miller and Sellers 1990).

Other environmental factors besides hunting pressure can affect composition of a bear population. For example, the proportion of single bears in a population may be increased if productivity of the population is low because of nutritional stress (e.g., a berry crop failure) or very high mortality of juveniles. Consequently, the proportion of single bears is likely to be useful only as an index for detecting large changes in hunting pressure.

The proportion of subadults in the MRSGS population during 1976-88 averaged 16% and did not differ between a period of relative stability (1976-84) and the period of population growth (1985-88) (x^2 = 0.47, df = 1, P = 0.49). Once the population peaked in 1989, and for the next 2 years, subadults accounted for a significantly smaller proportion (8%) of the population (x^2 = 12.89, df = 1, P < 0.001).

Adult Survival Rates

Death of an adult was assumed if the bear was deemed "recognizable," had been identified at McNeil for at least 2 years, and then was absent for 2 or more years (i.e., an identifiable bear seen up until 1989 was presumed dead if it did not return in either 1990 or 1991). Several known bears skipped 1 year at McNeil, but no recognizable bear was ever absent for 2 years and subsequently returned. From 1980 to 1989 adult females had a 0.93 annual survival rate based on 11 presumed deaths from 168 adult female bear-years, and adult males had a 0.94 survival rate (Table 2).

Reproduction and Recruitment

Litter Size.—Litter sizes for the first seasonal observation of families were compared for 3 time

Table 2. Survival estimates for recognizable adult brown bears at McNeil River, Alaska, 1980-89.

	Males				Females			
Year	No. at risk	No. of deaths	Survival estimates	95% CI	No. at risk	No. of deaths	Survival estimates	95% CI
1980	12	0	1.00	1.00-1.00	11	0	1.00	1.00-1.00
1981	16	4	0.75	0.57-0.93	11	3	0.73	0.50-0.95
1982	12	0	1.00	1.00-1.00	15	0	1.00	1.00-1.00
1983	15	1	0.93	0.81-1.00	16	0	1.00	1.00-1.00
1984	14	0	1.00	1.00-1.00	17	1	0.94	0.83-1.00
1985	20	0	1.00	1.00-1.00	17	2	0.88	0.74-1.00
1986	25	0	1.00	1.00-1.00	19	1	0.95	0.85-1.00
1987	29	2	0.93	0.84-1.00	19	1	0.95	0.85-1.00
1988	29	2	0.93	0.84-1.00	20	2	0.90	0.78-1.00
1989	33	3	0.91	0.82-1.00	23	1	0.96	0.88-1.00
Total	205	12	0.94	0.91-0.97	168	11	0.93	0.90-0.97

periods. Glenn et al. (1976: 389) reported cub litter sizes averaged 2.1 for 1963-72 ($n = 41$). From 1973 to 1984 when the population was relatively stable, the average cub litter size was 2.11 ($n = 47$ litters). Thereafter (1985-91) the population increased and stabilized, and the average litter size was 2.24 ($n = 49$ litters). Average yearling litter sizes were 1.80 ($n = 69$), 1.93 ($n = 29$) and 1.88 ($n = 41$) for the same three time periods. Average size for litters 2.5 years or older was 1.91 for 1973-91 ($n = 33$). Litter size did not differ between the 2 periods 1973-84 and 1985-91 when total population size and number of adult males were different (cubs: $t = 0.81$, 94 df, $P > 0.20$; yearlings: $t = 0.30$, 68 df, $P > 0.50$).

Substantial mortality, especially for cubs, occurs within the first month after den emergence (Miller 1988). The date when litters were first observed has a direct bearing on litter size. For recognizable females from 1980 to 1991, cub litters ($n = 67$) averaged 2.15 when first seen (mean date of 14 Jul, range 23 May-13 Aug) approximately 1.5 months after den emergence. By the time these litters were last seen an average of 1 month later, the mean litter size had declined by 7% to 2.00, (not counting the loss of entire litters).

Female Age Versus Litter Size.—Mean size for first litters (1.8, $n = 22$) was smaller than subsequent litters (2.5, $n = 33$) ($t = 3.64$, 54 df, $P < 0.001$) until females reached 23 years of age (Table 3). Only 1 of 4 litters produced by females older than 23 years had more than 1 cub.

Survival of Cubs and Yearlings.—Past studies have

compared average litter sizes of cubs and yearlings to estimate mortality; however, unless the number of entire litters that are lost are included, the mortality rate is underestimated (Bunnell and Tait 1985). For instance, combining all data from 1963 to 1991 at MRSGS, average litter size declined by 18% between 0.5 and 1.5 years of age. This does not take into account loss of entire litters. Using only recognizable females at MRSGS, 11 of 64 litters (17%) were lost between the time they were first seen as cubs and last seen as yearlings. Thus, actual mortality is about twice the rate as suggested by the change in average litter size.

A more accurate estimate of cub loss is obtained by following individual litters. In updating Glenn et al. 1976, Modafferi (1984) reported 31% mortality between the ages of 0.5 and 1.5 (15 of 48 cubs). From 1978-91, 37 of 120 cubs (31%) disappeared (Table 4). Other Alaskan studies, where cub litters were typically observed shortly after den emergence, reported cub mortality rates of 33% in southcentral Alaska (Miller 1988, $n = 107$), 29% in northcentral Alaska Range (Reynolds 1993, $n = 52$), and 37% on Kodiak Island (Smith and VanDaele 1991, $n = 56$). If cub litters at McNeil had been observed earlier in the spring, the observed mortality rate probably would have been higher.

The Kaplan-Meier procedure was applied to observations made at MRSGS from 1980 to 1991 when daily records of recognizable bears were kept. Based on 4,636 cub observation days, cub survival was 0.67

Table 3. Sequential cub litter sizes and birth intervals for recognizable brown bears at McNeil River, Alaska, 1963-91.

Bear	Litter number (age of mother)						
	1st [a]	2nd	3rd	4th	5th	6th	7th
Lan	1 (5)	3 (9)	2 (12)	3 (17)	3 (20)	2 (23)	1 (26)
Spo	1 (5)	3 (8)	3 (11)	2 (15)	4 (22)		
Reg		2 (14)	1 (18)	1 (20)	1 (24)		
Jea	2 (6)	3 (9)	1 (12)	3 (17)	1 (21)		
Rdc		3 (7)	3 (13)	4 (17)	1 (23)		
Bgm		3 (12)	3 (15)	3 (20)			
Whit	2 (7)	3 (10)	3 (15)	3 (21)			
Mel	1 (~6)[b]	2 (9)	3 (11)				
Dug	1 (~6)[b]	1 (9)	3 (12)				
Har	1 (8)	1 (11)					
Od		2 (8)	1 (11)				
Ted	1 (6)	3 (11)					
Tee	2 (~8)[b]	3 (12)					
Msm	3 (~9)[b]	3 (14)					
Rol	2 (~10)[b]	3 (14)					
Zar	1 (7)	3 (11)					
Ani	3 (~6)[b]	2 (10)					
Red	2 (6)						
Blu	1 (9)						
Mcb	3 (~9)[b]						
Hol	1 (~6)[b]						
Wai	3 (~7)[b]						
Lel	2 (7)						
05	2 (5)						
Fos	2 (~6)[b]						
Sno	2 (~6)[b]						
Rgn	none by ~7[b]						
Tin	none by ~12[b]						
Mean litter size	1.77	2.52	2.30	2.71	2.00	2	1
Mean birth interval	3.7	3.3	4.4	4.8			

[a] Only known litters are included in this column.

[b] Ages preceded by ~ were estimated while bear was a subadult.

between first and last observation during the summer season (Table 5). From the last observation of cub litters until they were first observed as yearlings, an additional 19.8% of cubs were lost. This combines to a maximum survival rate of 0.53 between 0.5 to 1.5 years of age.

Summer survival rate for yearlings was 0.89 (Table 6) based on 4,239 yearling observation days. We could not calculate survival from 1.5 to 2.5 years of age because many family breakups occurred before arrival

Table 4. Survival of brown bears from 0.5 to 1.5 years of age at McNeil River, Alaska, 1978-90.

Year	No. of Litters	No. of cubs	Deaths		Survival estimate
			First summer	First winter	
1978-79	2	8	0	5	0.38
1979-80	2	4	2	0	0.50
1980-81	3	7	0	1	0.86
1981-82	2	3	0	0	1.00
1982-83	2	6	0	0	1.00
1983-84	2	2	0	1	0.50
1984-85	5	9	0	0	1.00
1985-86	6	11	0	3	0.73
1986-87	5	10	0	2	0.80
1987-88	7	16	4	1	0.69
1988-89	7	19	1	3	0.79
1989-90	6	15	2	0	0.87
1990-91	4	10	3	3	0.40
Total	53	120	12	25	0.69

at MRSGS in their third summer.

Comparison Between Survival Estimates.—The 3 methods used above give different estimates of survival between 0.5 and 1.5 years of age. The first 2 provide an estimate of percentage of cubs that die, while the Kaplan-Meier technique estimates survival rate. The Kaplan-Meier method allowed staggered entry and censorship for families under observation for various lengths of time. However, this method may overrepresent early mortality when it is disproportionately high and sample sizes are small because the survival rate for the first period is carried through the remainder of the observation periods. For example, if during the first time period only 4 cubs are under observation, and 1 cub is lost, the survival rate starts at 0.75 and will only get lower even as the sample size increases and the time-specific mortality rate decreases.

All 3 methods overestimated first year survival because mortality during the first 1-2 months after den emergence was not measured. Females with cub litters tend to remain at higher elevations after den emergence than when they have older litters or are alone (Miller et al. 1987). This may serve as an isolation mechanism to avoid the threat posed by other bears. At MRSGS the mean date of arrival for 24 females with a total of 43 cub litters was 15 July (range 6 May-13 Aug).

These same females arrived an average of 18 days earlier in subsequent years when they had yearling litters. The magnitude of the unmeasured mortality between den emergence and arrival at MRSGS is likely to be substantial based on radio-telemetry studies in Alaska. Miller (1988) reported 77% (23 of 30) of cub deaths occurred during spring.

Reproductive Interval, Total Production, and Longevity.—Birth interval was based on the number of years between cub litters regardless of the fate of the litter. The birth interval of 17 females for successive litters averaged 3.7 ($n = 13$), 3.5 ($n = 10$), 4.4 ($n = 7$), and 4.8 ($n = 5$) (Table 2). Only 1 female produced more than 5 litters. The shorter birth intervals for first and second litters may have been due to higher mortality of entire litters causing the female to breed on a shorter rotation than if the litter had been raised to normal weaning age. The reproductive interval between successful litters, i.e., those raised at least to the end of the second summer, was calculated for 20 females (each present for at least 6 years) observed for a total of 242 bear-years. These females produced 83 yearlings in 47 litters, for an average reproductive interval of 5.15 years and overall recruitment rate of 0.34 yearlings/adult female/year. Ideally, reproductive interval and recruitment rate are calculated based on the period between successful weaning of litters, but this was not possible because weaning normally occurred in the spring prior to arrival at McNeil.

Total lifetime productivity was recorded for 11 females followed from reproductive maturity to presumed death. These bears lived from 6 to 25 years (mean age at death = 11.7 years). These 11 bears raised a total of 21 yearlings (mean lifetime productivity = 1.9). In 1991 a 26-year-old bear produced her seventh litter.

Effects of Increased Population Size on Recruitment

Several measures were used to test hypotheses about the relationship between increasing population size and number of adult males on productivity and recruitment. We found a positive correlation between the number of adult males and the total number of young accompanying females during 1976-91 ($r_s = 0.66$, $P < 0.01$). Because of several documented cases of intraspecific predation by adult females (P. Hessing and L. Aumiller, Alaska Dep. of Fish and Game, unpubl. data), we also regressed total adults against the total number of dependent young and again found a positive correlation ($r_s = 0.71$, $P < 0.005$). The percentage of

Table 5. Kaplan-Meier cumulative survival estimates for brown bear cubs at McNeil River, Alaska, 1980-91.

Dates	No. cubs days	No. at risk	No. of deaths	No. censored	No. new added	Survival	95% CI
23 May-5 June	42	3	0	0	3	1.00	1.00-1.00
6 Jun-13 Jun	48	6	0	0	3	1.00	1.00-1.00
14 Jun-20 Jun	68	12	1	0	7	0.89	0.65-1.00
21 Jun-27 Jun	107	16	2	0	6	0.77	0.52-1.00
28 Jun-4 Jul	189	33	0	0	17	0.77	0.59-0.95
5 Jul-11 Jul	297	51	1	0	19	0.75	0.61-0.89
12 Jul-18 Jul	474	84	0	1	34	0.75	0.64-0.86
19 Jul-25 Jul	653	101	5	0	22	0.71	0.60-0.81
26 Jul-1 Aug	801	115	5	6	26	0.68	0.58-0.78
2 Aug-8 Aug	724	85	2	32	0	0.67	0.53-0.78
9 Aug-15 Aug	496	62	0	23	2	0.67	0.53-0.80
16 Aug-31 Aug	578	11	0	51	0	0.67	
1 Sep-19 Sep	159	2	0	11	0	0.67	

Table 6. Kaplan-Meier Cumulative survival estimates for brown bear yearlings at McNeil River, Alaska, 1980-91.

Dates	No. Yearling Days	No. at risk	No. of deaths	No. censored	No. new added	Survival	95%CI
15 May-5 Jun	112	8	0	0	8	1.00	1.00-1.00
6 Jun-12 Jun	109	17	0	0	9	1.00	1.00-1.00
14 Jun-20 Jun	183	33	0	0	16	1.00	1.00-1.00
21 Jun-27 Jun	242	37	3	0	9	0.91	0.79-1.00
28 Jun-4 Jul	311	49	1	0	11	0.89	0.78-1.00
5 Jul-11 Jul	421	64	0	4	19	0.89	0.81-0.98
12 Jul-18 Jul	558	94	0	0	30	0.89	0.81-0.98
19 Jul-25 Jul	648	90	0	6	2	0.89	
26 Jul-1 Aug	571	75	0	15	0	0.89	
2 Aug-8 Aug	456	57	0	18	0	0.89	
9 Aug-15 Aug	291	37	0	20	0	0.89	
16 Aug-31 Aug	274	8	0	29	0	0.89	
1 Sep-16 Sep	63	1	0	8	0	0.89	

adult females that had dependent offspring showed no relationship to the number of adult males or total adult population size (r_s = 0.06 and 0.04, respectively, $P >$ 0.05). Because most mortality occurred during the first year of life, we compared yearlings/adult female (our best measure of recruitment) versus the number of adult males and total adults recorded the previous year. No relationship was found (r_s =0.05 and 0.12,

respectively, $P >$ 0.50). These results do not support a density-dependent suppression of recruitment.

Density-dependent mechanisms affecting subadult survival or dispersal may have resulted in a stable number and declining proportion of subadults using MRSGS after the population peaked in 1989. We could not determine the fate of subadults that disappeared from MRSGS, so we were unable to further explore

this possible means of population regulation.

If and how compensatory, density-dependent mechanisms operate in brown bear populations is important both for managing exploited populations and for understanding the dynamics of protected populations. Conflicting evidence exists about the influence of population size and proportion of adult males on productivity and survival (McCullough 1981, Stringham 1983, Miller 1990b, McLellan 1994). Although we could not demonstrate a relationship between increased population size or number of adult males and reduced productivity or cub survival, we did find low reproductive rates, due primarily to high cub mortality and long reproductive interval.

Effects of Salmon Escapements on Cub Production and Survival

The influence of salmon availability on reproductive success and cub survival was assessed from 1971 to 1991. Comparisons of escapements with cub survival, the subsequent year's cub litter size, and percent adult females with cubs all showed no correlation ($r^2 = 0.08$, 0.03, and 0.14, respectively).

Measurement of the effect of salmon abundance on reproductive parameters is complicated because availability of salmon to bears is as much dependent on water level, which affects the salmons' vulnerability, as on escapement size. Furthermore, the McNeil bear population has access to other food resources, including several other salmon runs. Given the small sample sizes of cubs (range 2-19 annually), prolonged period of association between females and their offspring, and rather random fluctuations in escapement size, it is not surprising that correlations are absent. We do not discount the importance of nutrition on productivity.

CONCLUSIONS

The number of bears observed at MRSGS increased from an average of 66 during 1969-84 to an average of 113 from 1987 to 1991. Reproductive rate and cub survival rate did not show a density-dependent effect, but the overall recruitment rate of young through their second summer was very low (0.34 yearling/adult female/year) due to high cub mortality and long reproductive interval. During the period when the number of bears seen at MRSGS increased, there was a decrease in the proportion of subadults in the population. This suggests that subadult dispersal and/or mortality may be a major component of population regulation in high-density populations minimally influenced by human-caused mortality.

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