

# BLACK BEAR REPRODUCTION AND CUB SURVIVORSHIP IN SOUTH-CENTRAL ALASKA

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*Abstract:* Reproductive data collected during a period of 11 years are presented for a low-density black bear (*Ursus americanus*) population occupying marginal habitat along the Susitna River. These data are contrasted with data from higher-density populations on the Kenai Peninsula also in south-central Alaska (Schwartz and Franzmann 1991), thought to occupy better habitat. Low reproductive and recruitment rates and high cub mortality rates were found in the Susitna population. Mean litter size was 2.1 for newborn cubs (range = 1-4), and 1.9 for yearlings, and sex ratio for cubs or yearlings were not different from 50:50 ( $P > 0.10$ ). Mean age of first reproduction was 5.9 years (range = 5-7), recruitment interval was 2.7 years (range = 2-5), birth interval was 2.03 years (range 1-4), and 59% of newborn cubs survived for 1 year (survivorship = 0.54, 95% CI = 0.42-0.66). A large proportion of adult females were without cubs following an apparent berry crop failure and again 5 years later. This generated pulses of cubs produced 2-3 years and 6-7 years after the berry crop failure. First year survivorship in the Susitna population was lower than in the 2 Kenai populations studied by Schwartz and Franzmann (1991) ( $P = 0.06$  and  $< 0.01$ ). The parameters in the 3 Alaskan populations that varied in response to different environmental conditions were first year survivorship, recruitment interval, and age at first reproduction; litter size was not responsive. For purposes of population modeling, recruitment interval will usually be a more useful statistic than birth interval because of early mortality of entire litters. In the Susitna area, black bear productivity and calculated consumption rates of moose calves were similar to findings in the least productive Kenai population. The Susitna data were consistent with the hypothesis of Schwartz and Franzmann (1991) that productivity in Kenai bears was dependent on calf consumption rates during spring.

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Black bear reproductive and survivorship rates are affected by availability and quality of food (Jonkel and Cowan 1971; Rogers 1976, 1983, 1987; Beecham 1980; Reynolds and Beecham 1980; LeCount 1982; Hugie 1982; Eiler et al. 1989; Elowe and Dodge 1989; Kolenosky 1990; Beck 1991; Schwartz and Franzmann 1991). Most studies of these relationships have focused on year to year variability within the same geographic area, but some (e.g. Beecham 1980, Hugie 1982, Schwartz and Franzmann 1991) have examined geographic variability in these rates. In the first extensive study of black bear ecology in Alaska, Schwartz and Franzmann (1991) concluded that productivity in 2 south-central Alaska populations was correlated with springtime consumption of moose calves and that these consumption rates, in turn, were correlated with successional stage following wildfires that influenced numbers of moose calves available to bears.

Most black bear studies have been conducted in areas with moderate to high densities of bears. Standardized, generally accepted black bear density estimation techniques are not available and this makes comparisons of densities in different areas difficult. However, in a list of 20 black bear density estimates throughout North America compiled by Beck (1991), the average density was 299 bears/1,000 km<sup>2</sup> (range = 59-588, SD = 154) and only 3 areas, including the Susitna area examined in this report, had densities < 100 bears/1,000 km<sup>2</sup>. The lowest density population in this list (59 bears/1,000 km<sup>2</sup>) was a heavily-hunted population in Arizona where only 60% of cubs survived their first year of life (LeCount 1987). The other low-density

population was lightly exploited in relatively poor habitat in Maine (Hugie 1982); data on cub survivorship in this area were not reported. Low density (90/1,000 km<sup>2</sup>) but no other information was also reported for a black bear population in Colorado's Rocky Mountain National Park (H. McCutchen unpubl. data, cited in Beck 1991).

Few black bear studies have been conducted at high latitudes. The current study in the Susitna River area is, to my knowledge, the northernmost study of black bear reproduction. The Susitna population is also characterized by low density (90 bears/1,000 km<sup>2</sup> [Miller 1987]). This area is 260 km farther north than the moderate-density (200 bears/1,000 km<sup>2</sup>) Alaskan black bear populations studied by Schwartz and Franzmann (1991) during an overlapping time period. Their Kenai study used density estimation, survivorship, and reproductive rate enumeration techniques that were directly comparable to those reported here.

The opportunity to study this low-density black bear population resulted from a proposal to build a large hydroelectric project on the Susitna River. An initial brown bear (*Ursus arctos*) study was expanded to include black bear when it became clear there were significant numbers of black bears in the area that would have been impacted by the proposed, but never built, dam. These circumstances provided a rare opportunity to study a low-density black bear population that was functioning naturally under conditions with minimal human impact. The upstream portion of my study area was defined as marginal habitat in the sense that the area upstream and away from the study area was treeless and occupied primarily by brown bears,

and because of the unavailability of at least 1 key food (American devils club, *Oplopanax horridus*) used extensively by black bear populations farther downstream and in more southern habitats (Schwartz and Franzmann 1991).

Objectives of this study were to (1) estimate productivity and survivorship parameters needed to establish sustainable harvest levels for low-density black bear populations in the interior of Alaska and similar areas, (2) identify similarities and differences between productivity and survivorship in this population and the 2 Kenai Peninsula populations studied by Schwartz and Franzmann (1991), (3) determine if the Susitna data are consistent with the hypothesis of Schwartz and Franzmann (1991) that black bear productivity is directly correlated with consumption of moose calves during spring, and (4) evaluate the impact of an apparent berry crop failure on black bear productivity in subsequent years. Raw data for the comparisons reported here were presented in Miller (1992:Appendix C).

The assistance of D. McAllister was of critical importance in collection of the data reported in this study. Other Alaska Dept. of Fish and Game (ADF&G) staff who made significant contributions were W. Ballard, C. Gardner, M. McDonald, K. Schneider, C. Schwartz, B. Strauch, B. Taylor, R. Tobey, and T. Wettin. E. Becker assisted with statistical analyses. C. Schwartz, M. Pelton, and an anonymous referee offered valuable comments on earlier drafts of this manuscript. My thanks to C. Schwartz for reading this paper at the Missoula conference. Fixed- and rotary-wing aircraft were flown by pilots from McMahan Flying Service, Kenai Air Alaska, Southcentral Air, Lee's Air Taxi, Deering Air Taxi, Wiederkehr Air Inc., and Sportsman's Flying Service. Alaska State Senator Rick Halford allowed us to use his landing strip and other facilities at Susitna Lodge. During 1980-86, this study was funded by the Alaska Power Authority as part of assessment studies for the proposed Susitna Hydroelectric project; subsequently it was funded by the State of Alaska and Federal Aid to Wildlife Restoration Job 4.21.

## STUDY AREAS

The Susitna study area was along an approximately 110-km long section of the Susitna River drainage in the Talkeetna Mountains of south-central Alaska (Fig. 1). The center of the study area was at 62°45' north latitude and 149°30' west longitude. The total study area was 4,900 km<sup>2</sup> and included 2 adjacent areas

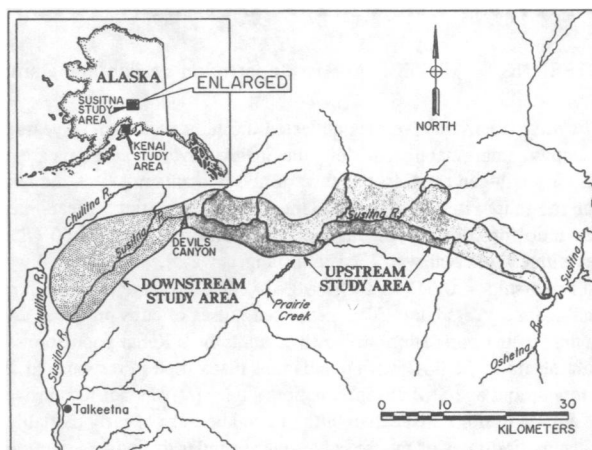


Fig. 1. Location of the Susitna study area in south-central Alaska and the comparison study areas on the Kenai Peninsula studied by Schwartz and Franzmann (1991).

that differed in degree of hunting effort and some habitat components. The area was mountainous with elevations ranging from 300 to 2,300 m. Precipitation averaged 80 cm/year, mostly as snow during the winter.

Denning ecology of black bears in the Susitna and Kenai study areas discussed in this report was described by Schwartz et al. (1987).

## Upstream Susitna Study Area

The primary effort was in an upstream study area above Devils Canyon and below the confluence of the Susitna and Oshetna Rivers (Fig. 1). Bears ( $n = 32$ ) were captured, radiomarked, and relocated in a 1,120 km<sup>2</sup> area along an approximate 87 km section of the Susitna River in this upstream area. Movements of these bears based on 2,195 radio locations during 1980-85 described an upstream study area of 2,950 km<sup>2</sup> (Miller 1987) (Fig. 1). The Susitna River in this area flows through a broad (15-20 km) valley but black bears were largely confined to forested habitats that occurred only within 1-2 km of the Susitna River and its tributary streams. Black bears occasionally ranged into open brushy and upland tundra zones at higher elevations away from the river especially during the late summer when berries (*Vaccinium ovalifolium*, *V. vitis-idaea*, *Empetrum nigrum*) were ripening. Forests were predominantly black spruce (*Picea glauca*) and white spruce (*P. mariana*) intermixed with paper birch (*Betula papyrifera*) and a few stands of poplar (*Populus tremuloides*). The brush zone was predominantly alder (*Alnus* spp.), dwarf birch (*Betula glandulosa*), and willow (*Salix* spp.). On the Susitna River, very few

salmon (*Oncorhynchus* spp.) were able to navigate the rapids at Devils Canyon into the upstream study area. During July a tributary of the Talkeetna River, Prairie Creek (Fig. 1), contained abundant king salmon (*O. tshawytscha*) within 4-5 km of the upstream study area but no radio-marked black bears moved to this stream possibly because of competitive exclusion by the many brown bears (Miller 1985, 1987). American devils club was very rare in the upstream area. Moose (*Alces alces*) and brown bear were abundant in this study area, caribou (*Rangifer tarandus*) were seasonally abundant in the upstream portions of the area, and dall sheep (*Ovis dalli*) were uncommon. Human access to the upstream area was largely by aircraft and there was little black bear hunting.

### Downstream Susitna Study Area

The downstream study area extended along an approximately 24-km length of the Susitna River in a relatively narrow valley (4-10-km wide) below Devils Canyon (Fig. 1) where 22 black bears were captured and radiomarked. The downstream study area was 1,950 km<sup>2</sup> defined by 616 radiolocations of these bears during 1982-85 (Miller 1987). Forest cover was dominated by white and black spruce with black cottonwood (*Populus trichocarpa*) on riparian lowlands.

Alder thickets dominated slopes on both sides of the valley. Compared to the upstream area, this portion of the study area was extensively vegetated with shrubs (predominantly alder) and spruce-birch forests. Open tundra habitats were confined to small areas on the tops of surrounding mountains and ridges. Habitat in the downstream study area was more typical of black bear habitat in this portion of south-central Alaska. Moose and brown bears were less abundant in this area than in the upstream area and caribou were absent. American devils club was more abundant especially in riparian areas. Four species of Pacific salmon could be found in spawning sloughs in this area but analysis of bear scats picked up along these sloughs during July indicated that American devils club berries were greatly preferred over salmon (Miller 1987). Up the Susitna River from Talkeetna to Devils Canyon, access by riverboat was easy and black bears were heavily hunted.

### Kenai Studies

Comparable data were collected from black bear populations in the north-central lowlands (35-90 m elevation) of the Kenai Peninsula (Schwartz and Franzmann 1991) (Fig. 1). Vegetation in this area, as in the downstream Susitna area, was northern boreal

spruce forest. Climate was less severe than in the Susitna because of the maritime influence. On the Kenai, Schwartz and Franzmann (1991) reported differences in black bear reproductive rates in 2 areas that differed in successional stages following wildfires in 1947 and 1969.

## METHODS

### Capture, Marking, and Monitoring

Most bears were captured during annual capture efforts in May and June (1980-85). Bears were spotted from fixed-wing aircraft (PA 18), immobilized by darts fired from a helicopter, and, where appropriate, fitted with radio-transmitter collars (Telonics, Mesa, Ariz.) (Miller 1987). Age was determined from cementum annuli in a premolar tooth. Transmitters of radio-marked bears were replaced at 2-3 year intervals during spring capture operations or during March and April while bears were in winter dens. All adults were radiomarked. Collars of radio-marked subadults had canvas spacers designed to rot through within 18 months permitting the collar to fall off if not replaced. During 1980-85, radio-marked bears were located from fixed-wing aircraft approximately every 10 days between the periods of den emergence and entrance (Schwartz et al. 1987). Number and age of offspring observed with radio-marked females were recorded during monitoring flights and during visits to dens. During 1986-90, the reproductive status of bears with still-functioning radio transmitters was monitored 1-3 times following emergence from dens in the spring, 1 time in mid-summer, and 1-2 times prior to den entrance. All transmitters had ceased functioning by 1991 when this study terminated.

### Reproductive Parameters

Litter size data were based on the earliest observation of a complete litter. In most cases this observation was made when bears exited from dens. In some cases the first observation of a litter was obtained earlier, within dens of radio-marked bears.

Age at first reproduction was estimated by annual observations of radio-marked subadults and by backdating litters with 5- or 6-year-old females. Data were augmented for subadult females that had not produced litters but were older than the mean age of females that had by assuming these females would produce a litter the following year. Simulation studies demonstrated that these procedures provided more accurate estimates (Miller 1993).

Recruitment interval was defined as the period between production of a litter that successfully reached the age of separation from its mother (at least 1.5 yr) and the production of the next litter that reached yearling age or was still with its mother at an older age. With this approach, the loss of a litter of cubs in their first year of life was equivalent to not producing a litter. In illustration, a female that separates from yearlings in year (x), gives birth but loses litters in years (x+1) and (x+2), and produces a litter in (x+3) from which it separates during (x+4) would be counted as having had 1 four-year recruitment interval. There would be 3 reproductive intervals for these same data, 2 of 1 year and 1 of 2 years. Recruitment interval for first litters were counted from the year of first litter production to the year when offspring first separated from their mothers at minimum age of recruitment (1.5 or older). During each year of study, data for incomplete intervals >2 years were included by assuming the litter would be recruited the following year (Miller 1993).

### Calf Moose Consumption

Number of calf moose eaten per bear (yearling or older) in the upstream Susitna study area was calculated following procedures outlined by Schwartz and Franzmann (1991:Appendix F). Input into these calculations included moose herd composition data (bulls = 15%, calves = 21.6%, cows older than calf = 63.4%, adult females = 53.7, yearling females = 9.7%) obtained from autumn 1984 aerial surveys in Count Area 7, which overlaps a portion of the upstream study area (Ballard et al. 1991). Sex ratio of moose calves at birth was 0.5, moose density was 1.34/km<sup>2</sup> in 1984, and estimated calf production was 1.26 calves/females older than yearling (Ballard et al. 1991). Black bear predation accounted for the deaths of 4 of 46 (8.7%) radio-marked newborn moose calves during spring 1984 (Ballard et al. 1990). Black bear density (yearlings and older) was estimated at 15.4 km<sup>2</sup>/bear (Miller et al. 1987).

Comparable moose data were not available for the downstream Susitna study area.

### Comparison With Kenai Studies

The only study of black bear reproductive rates conducted in Alaska was on the Kenai Peninsula (Fig. 1) (Schwartz and Franzmann 1991). This study compared 2 study areas at different stages of phenology following wild fires (the 1947 and 1969 burns). Statistical comparisons for these areas made by Schwartz and Franzmann (1991) were standardized on

the period when both areas were studied (1982-87). Schwartz and Franzmann (1991) also presented data from the 1947 burn area collected prior to the period both areas were studied. Data from the whole period of study in the 1947 burn areas (1978-87) were used to make comparisons with reproductive data in the Susitna study area. Inclusion of these earlier years tended to make the data from the 2 Kenai study areas more similar than the comparisons reported by Schwartz and Franzmann (1991), perhaps because food supplies were relatively better during these early years.

### Mortality

Mortality was assumed when offspring of radio-marked females disappeared between the time of first observation of a litter of newborns in dens or immediately following emergence from dens, and emergence of the marked female from its den the following year when offspring would be 1.4 years old. Survivorship was calculated using the staggered entry design described by Pollock et al. (1989).

### Statistics

The null hypothesis that the proportion of adult females without offspring was the same in all years was analyzed with Fisher's exact test (StatXact, Crystal Corp. Inc). Adjusted residuals used to determine cells that contributed most to rejection of the null hypothesis were calculated according to Everitt (1977:47). Mann-Whitney U tests (Conover 1980) were used to test null hypotheses that mean age at first reproduction and reproductive interval were different in different study areas. Wilcoxon rank sum or Kruskal-Wallis tests were used to compare litter sizes between different areas (Conover 1980).

## RESULTS

### Population Composition and Density

Density was estimated using modified capture-mark-resight techniques at 90 bears of all ages/1,000 km<sup>2</sup> in the upstream area (95% CI = 77.4-102.1) (Miller et al. 1987). No density estimate was made in the downstream area but my subjective impression, in spite of the heavier hunting pressure, was that density in this area was 30-70% higher because of better habitat. There were more males in the upstream population than in the more heavily hunted downstream population. During the 1985 density estimate in the upstream area, 18 male and 17 female radio-marked bears ≥2 years old were present at least once in a 531 km<sup>2</sup> portion of

the upstream study area during an 11-day period in early June (Miller et al. 1987). In contrast, 4 males and 16 females  $\geq 2$  years old were captured in the downstream area during intensive capture operations in spring 1982 and 1983 (Miller 1987).

### Litter Size

In the Susitna study area, mean litter size for newborn cubs at the earliest observation (in the den or following emergence in the spring) was 2.12 (Table 1). Only 6.2% of litters had 1 cub (Table 1). Mean litter size for 19 litters observed in dens was 2.3 (range 2-4). Mean litter size for 43 litters of yearlings was 1.9 and 25.6% of yearling litters had a single offspring (Table 1). Litter size was smaller for yearling litters than for cub litters (1-tailed Wilcoxon rank sum test,  $P = 0.03$ ). This was because high cub mortality rates resulted in relatively more yearling litters with a single offspring than for litters of newborns. Mean litter size for 4 adult females accompanied by 2-year-old offspring was 2.0 (range 1-3).

All first litters of newborns observed had 2 cubs. As observed on the Kenai Peninsula by Schwartz and Franzmann (1991), in the Susitna area there was no

**Table 1. Comparison of black bear litter sizes in 3 Alaskan study areas.**

	Susitna <sup>a</sup> (1980-90)	1947 Burn <sup>b</sup> (1978-87)	1969 Burn <sup>b</sup> (1982-87)
<b>COY litters</b>			
Mean	2.1	2.1	2.3
Range	1-4	1-3	1-3
<i>n</i> =	65	46	27
Percent of size			
1	6.2	15.2	11.1
2	76.9	60.9	44.4
3	15.4	23.9	44.4
4	1.5	0	0
<b>Yearling litters</b>			
Mean	1.9	1.9	2.2
Range	1-3	1-2	1-3
<i>n</i> =	43	27	24
Percent of size			
1	25.6	22.2	20.8
2	58.1	66.7	37.5
3	16.3	11.1	41.7

<sup>a</sup> Includes upstream and downstream study areas.

<sup>b</sup> From Schwartz and Franzmann 1991 (Table 10).

difference between size of initial litter ( $n = 7$ ) and subsequent litters ( $\bar{x} = 2.14$ ,  $n = 58$ ) (2-tailed Wilcoxon rank sum test,  $P = 0.53$ ).

There were no significant differences between litter size of newborns in the Susitna study area and in the Kenai study areas (Kruskal-Wallis statistic = 3.99,  $P = 0.26$ ) (Table 1). All available data from the Susitna study and from the 1947 burn area were used for this test. Litter sizes were also not different during the standardized 1982-86 period in the 1947 burn ( $\bar{x} = 2.2$ , range 1-3,  $n = 30$ ) and in 1969 burn study areas ( $\bar{x} = 2.3$ , range 1-3,  $n = 27$ ) (Schwartz and Franzmann 1991).

### Cub Sex Ratio

In both Susitna study areas, sex ratio for newborn black bears examined in dens was 18 males:18 females. Sex ratio for newborns examined at earliest opportunity during 20 March-19 May was not significantly different from 50:50 (19 males:25 females,  $\chi^2 = 0.82$ , 1 df,  $P = 0.4$ ) (Miller 1987). Sex ratios for newborn cubs were also near parity on the Kenai Peninsula (15:20 in the 1947 burn [ $\chi^2 = 0.7$ ,  $P = 0.4$ ] and 27:24 in the 1969 burn [ $\chi^2 = 1.8$ ,  $P = 0.7$ ]) (Schwartz and Franzmann 1991). Sex ratio for yearling litters was also near parity in the Susitna (5:5), 1947 burn (7:13,  $\chi^2 = 1.8$ ,  $P = 0.2$ ), and 1969 burn (24:22,  $\chi^2 = 0.09$ ,  $P = 0.8$ ) study areas.

### Age at First Reproduction

In both Susitna study areas, combined mean age at first litter was 5.9 (Table 2). Age at first litter was 5 for 5 bears, 6 for 4 bears and 7 for 4 bears ( $\bar{x} = 5.9$ ). No bears had litters at age 3 or 4 ( $n = 2$  and 6 females available, respectively), 38% produced first litters at age 5 ( $n = 13$  bears of known status at that age), 75% had produced litters at age 6 or younger ( $n = 12$ ), 100% at age 7 or younger ( $n = 18$ ), and 100% at age 8 or younger ( $n = 25$ ). No females had failed to produce first litters when the study terminated.

**Table 2. Comparison of age of first litter in 3 Alaskan study areas.**

	Susitna <sup>a</sup> (1980-90)	1947 Burn <sup>b</sup> (1982-87)	1947 Burn <sup>b</sup> (1978-87)	1969 Burn <sup>b</sup> (1982-87)
Mean	5.9	5.8	5.1	4.6
Range	5-7	5-7	4-7	4-5
<i>n</i>	13	10	17	7

<sup>a</sup> Includes both upstream and downstream study areas.

<sup>b</sup> From Schwartz and Franzmann (1991:Table 8).

Age at first litter was different in the downstream Susitna area ( $\bar{x} = 6.8$ ,  $n = 4$ , range = 6-7) than in the upstream Susitna area ( $\bar{x} = 5.6$ ,  $n = 9$ , range = 5-7) ( $P = 0.02$ ). However, data were available from 10 five-year-old females in the upstream area compared to only 3 in the downstream area so this comparison may be biased by inadequate sample size. Correspondingly, data were combined for the 2 Susitna study areas in the above comparisons.

Mean age of first litter in the Susitna study area was different than on the Kenai Peninsula in the 1947 burn area (5.1 years during 1978-87,  $P = 0.04$ ) and from that in the 1969 burn study area (4.6 years during 1982-87,  $P < 0.01$ ) (Table 2). However, these differences between the Susitna and 1947 burn area did not exist ( $P = 0.74$ ) if data for the 1947 burn area were restricted to the 1982-87 standardized period when both Kenai areas were studied (Schwartz and Franzmann 1991) (Table 2). No bears had litters of newborn cubs at age 4 in the Susitna area, but many did in both Kenai study areas (Schwartz and Franzmann 1991).

### Recruitment Interval

Mean recruitment interval was 2.66 years (Table 3). This value includes data from 13 uncompleted intervals ( $\bar{x} = 3.46$  years, range = 3-5 years) that would have been at least as long as the mean value for the 37 completed intervals observed ( $\bar{x} = 2.37$  years, range = 2-5). Mean interval length was the same for upstream and downstream study areas ( $n = 34$  and 15, respectively,  $P = 0.5$ ) so data were combined.

Most completed intervals were 2 years ( $n = 28$ );

**Table 3. Comparison of black bear reproductive intervals between 3 Alaskan study areas. Reproductive interval was defined as the period between successive successful separation of yearling or older offspring and as the period between production of first litter and the next successful separation of offspring.**

	Susitna <sup>a</sup> (1980-90)	1947 Burn <sup>b</sup> (1978-87)	1969 Burn <sup>b</sup> (1982-87)
Mean	2.66	2.31	2.04
Range	2-5	2-3	2-3
<i>n</i>	50	35	25
% of intervals of length:			
2 years	56	69	96
3 years	26	31	4
4 years	14	0	0
5 years	4	0	0

<sup>a</sup> Includes both upstream and downstream study areas.

<sup>b</sup> From Schwartz and Franzmann (1991).

only 5 intervals were 3 years, 3 intervals were 4 years, and 1 interval was 5 years. The distribution of incomplete intervals  $\geq 3$  years was 8, 4, and 1 of 3, 4, and 5 years, respectively. Excluding intervals of 2 years, the mean for completed intervals (3.56 years,  $n = 9$ ) was the same as for incomplete intervals (3.46 years,  $n = 13$ ) ( $P = 0.8$ ); this suggests that the data from the individuals with incomplete intervals was not quantitatively different than from individuals with completed intervals.

I observed 25 recruitment intervals  $> 2$  years in the Susitna area. Skipping a year between litters was the most common cause for recruitment intervals  $> 2$  years ( $n = 18$ ). In 2 cases, long intervals resulted from skipping 2 years between litters of newborns. Intervals  $> 2$  years also resulted from delayed separation from mothers (at age 2) ( $n = 4$ ), and loss of 1 ( $n = 2$ ), or 2 ( $n = 2$ ) entire litters. Three bears that had intervals  $> 3$  years had a mixture of these reasons, this is why 28 reasons were counted for the 25 recruitment intervals  $> 2$  years.

Interval length in the 1947 burn area was longer than in the 1969 burn (Schwartz and Franzmann 1991), regardless of whether all the data from the 1947 burn were used ( $P = 0.02$ ) or just the data from 1982 to 1986 ( $P = 0.02$ ). Interval length in the Susitna area was not different from that in the 1947 burn during 1978-87 ( $P = 0.4$ ) but was longer than in the 1969 burn ( $P < 0.01$ ) (Table 3).

### Interval Between Yearling Litters

Mean interval between successive observations of Susitna females with litters of yearlings was 2.93 years (range 2-4,  $n = 14$  intervals). Five of these intervals were 2 years, 5 were 3 years, and 4 were 4 years. Longer intervals between litters of yearlings were evident in data from the Kenai Peninsula (Schwartz and Franzmann 1991). Mean interval between yearling litters in the 1947 burn was 2.38 years ( $n = 16$ , range 2-3); all 11 intervals in the 1969 burn area were 2 years.

### Birth Interval

Mean interval between successive production of litters of newborn cubs was 2.03 years ( $n = 32$ , range 1-4). There were 21 intervals of 2 years, 9 of 3 years, and 1 each of 1 and 4 years. The birth interval was less than the recruitment interval presented above (2.66 years) because of loss of entire litters.

### Patterns of Cub Production

Absent an environmental effect or loss of a litter,

adult female black bears should produce a litter of newborn cubs (COY) every other year, following separation from litters of yearlings. Environmental influences may cause bears to fail to produce litters every other year or cause early mortality of litters (Rogers 1976, LeCount 1980, Eiler et al. 1989). Based on atypically extensive movements of radio-marked black bears in late summer 1981, I suspected a failure of the berry crop, especially blueberries (*V. ovalifolium*) had occurred. This hypothesis was supported by a subjective on-ground inspection (Miller and McAllister 1982, Miller 1987). If failure of the berry crop influenced reproductive performance, this could be expressed through increased number of females without offspring in the year following the failure. An atypically large proportion of radio-marked adult females were without offspring in 1982, the year following the berry crop failure, and 5 years later in 1986 (Fig. 2). The null hypothesis that the same proportion of adult females were without offspring in each year was rejected ( $P < 0.01$ ). The cells that contributed most to the rejection were 1982 and 1986 when the fewest bears had offspring (adjusted residuals = 6.27 and 7.56, respectively). The next most significant cells were 1983 and 1988 when the fewest adult bears were without offspring (adjusted residuals = -4.39 and -3.11, respectively).

These data suggest a failure to produce COY litters

on schedule in the year following failure of the berry crop and, again, 5 years later. In the cases where status of adult females in 1981 was known, the open status of these in 1982 resulted from skipping a year following separation from yearlings or loss of COY litters in 1981 (the year of the berry crop failure) (Table 4). The open status of adult females in 1986 resulted from the same factors plus skipping a year following separation from 2-year-old offspring and from a previous "open" year (Table 4). During the course of this study, I observed 4 instances of females separating from 2-year-old offspring instead of yearling offspring; 3 of these instances occurred in the litters of COY produced in 1983, 2 years after the berry crop failure (Table 4).

### Moose Calf Consumption

Differences in consumption of moose calves were used to explain differences in productivity for 2 black bear populations on the Kenai Peninsula in south-central Alaska (Schwartz and Franzmann 1991). Using the same procedures (Schwartz and Franzmann 1991:Appendix F) data from our study area on moose population composition, moose density, bear density, and mortality rate to calf moose caused by black bears, were used to estimate 1.2 calves eaten per black bear (age  $\geq 1$ ). This estimated rate of consumption was equivalent to that estimated for the black bear population with relatively low productivity in the 1947

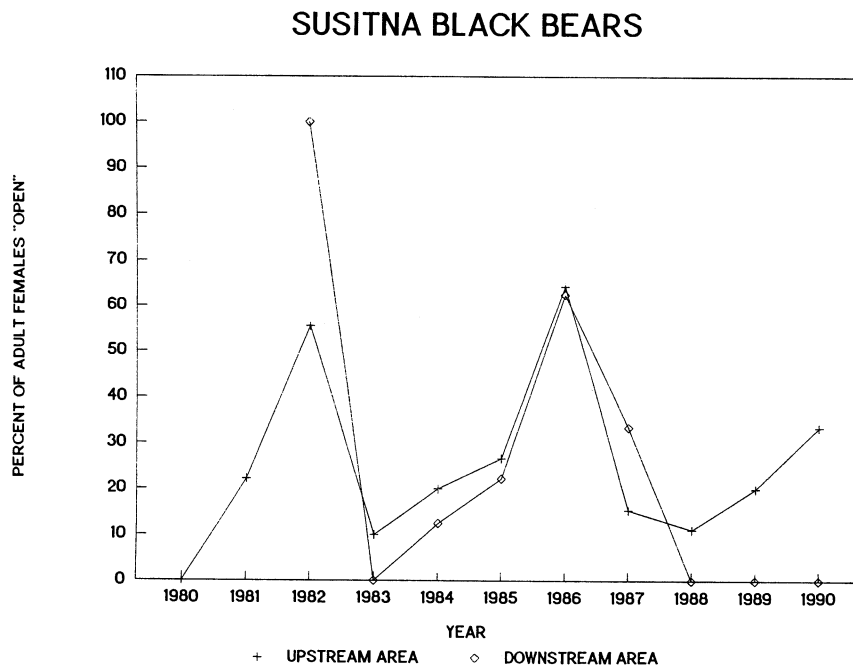


Fig. 2. Pulses in percent of black bear adult females without offspring ("open") following an apparent berry crop failure in 1981.

**Table 4. Number of adult female black bears without offspring ("open") in the Susitna study area of southcentral Alaska.**

Previous year's status	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	Total
Separation from yearling litter	0	1	3	0	1	1	5	1	1	1	0	14
Separation from litter of 2-year-olds	0	0	0	0	0	0	1	0	0	0	0	1
Loss of COY litter <sup>a</sup>	0	0	1	0	1	1	4	0	0	0	1	8
Also "open"	0	0	0	1	0	0	4	3	0	0	0	8
UNK.	0	1	5	0	1	4	0	0	0	0	0	11
Total for "open" bears	0	2	9	1	3	6	14	4	1	1	1	42
With litter of 2-year-olds	0	0	0	0	0	3	0	0	0	0	1	4
Subadult	1	2	6	6	3	1	1	--	--	--	--	20

<sup>a</sup> COY = cub-of-year.

burn study area on the Kenai Peninsula (1.4 [0.4-2.5]) and less than calf moose consumption for the black bear population exhibiting higher productivity in the 1969 burn study area (>5.4 [4.5-6.4]) (Schwartz and Franzmann 1991).

### Cub Mortality Rates

In the upstream study area, more cubs were lost during their first year (31 of 76) than in the downstream study area (1 of 23) ( $\chi^2 = 8.47$ , 1 df,  $P < 0.01$ ). These data are based on the period between first observation of a litter (in maternal den or immediately following emergence) and emergence from dens the following year. Causes of cub mortality were not determined but these differences may be related to more variable environmental conditions, to larger number of brown bears in the upstream area, or to the higher proportion of adult males in the lightly-hunted upstream area. Because of this difference in cub mortality, only the upstream area was used for the following analysis of survivorship rates.

Overall newborn survivorship in the upstream Susitna study area from first observation to exit from dens as yearlings was low (Table 5). Survivorship in the Susitna study area was lower than in either of the Kenai Peninsula study areas studied by Schwartz and Franzmann (1991) using data standardized for the same 1982-86 period ( $P < 0.10$ , Table 6). Using this same standardized period, cub survivorship on the Kenai was higher in the 1969 burn area than in the 1947 burn area (Schwartz and Franzmann 1991, Table 6). However, data were collected for a longer time in the 1947 burn area, and if all available data were used there would have been no difference in survivorship between the 2 Kenai areas (Table 7) ( $P = 0.32$ ). The above suggests

that there was a year effect on cub survivorship; during 1978-81 there was higher survivorship in the 1947 burn area than during the 1982-86 period when both areas were studied.

This year effect makes it problematic to compare survivorships between areas using different time periods. However, such comparisons may be useful for population modeling efforts in which it is necessary to input survivorship functions using all available data. Using all data available for each of the 3 study areas, cub survivorship in the Susitna area (0.58) was lower than in either Kenai area (Table 7) ( $P < 0.01$ ).

In both Susitna study areas, 17 litters with 40 newborns were observed both in dens during March-April and soon after emergence during mid-May. Two of these litters lost a cub between observation in dens and observation at emergence, 1 from a litter of 4 and the other from a litter of 3. This suggests a 5% in-den mortality rate during this period.

There was no difference in the likelihood of losing all or a portion of a litter of 1 or more newborns ( $\chi^2 = 0.89$ , 1 df,  $P = 0.35$ ). No cubs were lost from litters of >1 newborns ( $n = 4$ ). For 40 litters with more than 1 newborn cub, the whole litter survived in 22 cases, the whole litter was lost in 6 cases, and a portion of the litter was lost in 12 cases.

### DISCUSSION

Available techniques for monitoring trends in bear populations are expensive, typically imprecise, and may include bias (Harris 1986, Miller 1990). Because of problems in detecting trends, managers of exploited bear populations frequently use harvest models, in combination with population estimates, to calculate

**Table 5. Cumulative survivorship during 1980-90 of black bear newborn cubs with radio-marked mothers in the upstream Susitna River study area of south-central Alaska. Survivorship calculated using the technique of Pollock et al. (1989).**

Month	No. risk	No. deaths	Survival	No. censored	No. added	Variance (survivorship)	95% CI	
							Lower	Upper
In natal den	26	2	0.923	0	49	0.0025	0.825	1.022
May	73	2	0.898	0	0	0.0011	0.832	0.964
June	71	8	0.797	2	0	0.0018	0.713	0.880
July	61	10	0.666	1	0	0.0024	0.569	0.763
August	50	4	0.613	0	0	0.0029	0.507	0.718
September	46	4	0.560	3	0	0.0030	0.452	0.667
In next den	39	1	0.541	13	0	0.0035	0.430	0.661

harvest quotas (Bunnell and Tait 1980, Miller 1990). Good estimates of productivity and mortality rates are critical to such models (Bunnell and Tait 1980) as well as an understanding of what factors influence these parameters. Because bears have low reproductive rates compared to many other large mammals, accurate estimates of productivity require many years of study (Miller 1993).

Reproductive biology of black bears has been little studied in northern latitudes of North America. The current study is only the second in Alaska, and is also the northernmost study in North America to my knowledge. The other Alaskan study was conducted in 2 Kenai Peninsula study areas where black bear density was about 2.3 times higher than in my Susitna study area. In these study areas, Schwartz and Franzmann (1991) found that black bears in the area in a more advanced successional stage (the 1947 burn area) produced first litters at a later age and had a longer recruitment interval than in an area burned more recently (the 1969 burn area) but found no difference in litter sizes. Schwartz and Franzmann (1991) attributed these differences to greater availability and consumption of moose calves by black bears in the 1969 burn.

Bear productivity and consumption of moose calves in the Susitna and Kenai study areas were examined to see if the Susitna data were consistent with the relationship suggested by Schwartz and Franzmann (1991). The recruitment interval in the Susitna area was not different from that in the 1947 burn. The age of first litter was either older or the same in Susitna bears as in the 1947 burn depending on what time periods were compared. Both the Susitna area and the 1947 burn area had longer recruitment intervals and older age of first litter than in the 1969 burn. These results suggest that the factors that influence productivity for bears in the Susitna area are either similar or poorer than in the 1947 burn area and that both areas are poorer than in the 1969 burn area.

Calculated consumption of moose calves by black bears in the Susitna area was similar to that in the 1947 burn on the Kenai and lower in both areas than in the 1969 burn area. These productivity and moose calf consumption comparisons are consistent with the conclusion of Schwartz and Franzmann (1991) that differences in bear productivity in the Kenai populations reflected differences in moose calf consumption rates.

**Table 6. Comparison of newborn black bear cub survivorship (between exit from natal den and exit from dens as yearlings) using data collected during 1982 through 1986 in 3 south-central Alaska study areas.**

Area	No. of bears	No. of deaths	% censored	Survivorship	Variance	Comparison areas	Z statistic	P
1 - Susitna <sup>a</sup>	38	22	5.2	0.553	0.0053	1 v 2	-1.86	0.06
2 - 1947 burn <sup>b</sup>	30	9	1.7	0.742	0.0051	2 v 3	-1.96	0.05
3 - 1969 burn <sup>b</sup>	43	4	0	0.907	0.0020	1 v 3	-4.16	<0.01

<sup>a</sup> Upstream study area.

<sup>b</sup> From Schwartz and Franzmann (1991) and Schwartz (unpubl. data).

**Table 7. Comparison of newborn black bear survivorship (between exit from natal den and exit from dens as yearlings) using data collected during the entire period of study in 3 south-central Alaska study areas.**

May-Oct. data	No. of bears	No. of deaths	% censored	Survivorship	Variance	Comparison areas	Z statistic	P
1 - Susitna <sup>a</sup> (1981-90)	73	29	8.2	0.577	0.0037	1 v 2	-3.31	<0.01
2 - 1947 burn (1978-86) <sup>b</sup>	53	9	0	0.836	0.0024	2 v 3	1.09	0.28
3 - 1947 burn (1982-86) <sup>b</sup>	30	9	1.7	0.742	0.0051	3 v 4	-1.96	0.05
4 - 1969 burn (1982-86) <sup>b</sup>	43	4	0	0.907	0.0020	1 v 4	-4.37	<0.01
						1 v 3	-1.75	0.08
						2 v 4	-1.08	0.32

<sup>a</sup> Includes both upstream and downstream study area.

<sup>b</sup> From Schwartz and Franzmann (1991) and Schwartz (unpubl. data).

On the Kenai Peninsula, productivity was also influenced by year to year variability in black bear foods (Schwartz and Franzmann 1991). In the Susitna area, data on year to year variability in bear foods were not obtained but an apparent berry crop failure in 1981 appeared to result in few adult females accompanied by newborn cubs the following year and, again, in 1986. Many more females were accompanied by newborn cubs during the 1-2 years following the years when few offspring were produced. This suggests pulses of cub production may occur in the Susitna population 2-4 and 6-8 years after a berry crop failure. Many cubs born in years 2-3 after the berry crop failure would produce their own offspring 5-6 years later. This could contribute to and amplify the second peak in cub production.

Litter size was similar in the 3 Alaska studies. Sex ratio in newborn and yearling litters also did not vary from 50:50. These results suggest that these parameters were not affected by the factors that influence bear productivity in these Alaskan populations.

Although reproductive rates were similar in the upstream portion of the Susitna area and in the 1947 burn area, first year survivorship was much lower in the upstream Susitna area. Causes of cub mortality were not determined, but it is possible that there was more intra-specific predation by the greater number of brown bears in the upstream Susitna area than in the Kenai study area. The upstream Susitna area also was more lightly hunted and had a higher proportion of adult male black bears than the downstream area or Kenai areas, and this may have contributed to higher cub losses. However, the relationship between adult male abundance and cub survivorship is speculative and may not exist (Elowe and Dodge 1989, Miller 1991). First-year mortality in the Susitna study area was

generally higher than the typical 25-30% reported by Bunnell and Tait (1985) but low first-year survivorship was also observed in another low-density black bear populations (Elowe and Dodge 1989). In addition to low productivity, high first-year mortality may be instrumental in maintaining black bear populations in marginal habitat at low densities.

Recruitment interval, as defined here, has advantages over birth interval and interval between yearling litters in bear population models that require mean annual productivity rates. Birth interval may result in overestimation of productivity because of losses of complete litters. Data on intervals between yearling litters is slower to accumulate because it neglects the period between a bear's first litter production and its first successful weaning. In bears and other species with multi-year periods of maternal care, however, use of mean annual rates for productivity may misrepresent actual productivity (Taylor et al. 1987).

## LITERATURE CITED

- BALLARD, W.B., S.D. MILLER, AND J.S. WHITMAN. 1990. Brown and black bear predation on moose in southcentral Alaska. *Alces* 26:1-8.
- \_\_\_\_\_, J.S. WHITMAN, AND D.J. REED. 1991. Population dynamics of moose in south-central Alaska. *Wildl. Monogr.* 114. 49pp.
- BECK, T.D.I. 1991. Black bears of west-central Colorado. *Colorado Div. Wildl. Tech. Publ.* 39. 86pp.
- BEECHAM, J.J. 1980. Some population characteristics of two black bear populations in Idaho. *Int. Assoc. Bear Res. and Manage.* 4:201-204.
- BUNNELL, F.L., AND D.E.N. TAIT. 1980. Bears in models and reality—implications to management. *Int. Assoc. Bear Res. and Manage.* 4:15-23.
- \_\_\_\_\_, AND \_\_\_\_\_. 1985. Mortality rates of North

- American Bears. *Arctic* 38:316-323.
- CONOVER, W.J. 1980. *Practical nonparametric statistics*, 2nd ed. John Wiley and Sons, N.Y. 493pp.
- EILER, H.H., W.G. WATHEN, AND M.R. PELTON. 1989. Reproduction in black bears in the southern Appalachian mountains. *J. Wildl. Manage.* 53(2):353-3260.
- ELOWE, D.E., AND W.E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. *J. Wildl. Manage.* 53:962-968.
- EVERITT, B.S. 1977. *The analysis of contingency tables*. Halsted Press, John Wiley and Sons, N.Y. 128pp.
- HARRIS, R.B. 1986. Grizzly bear population monitoring: current options and considerations. Montana Forest and Conservation Expt. Station, School of Forestry, Univ. of Montana, Missoula Misc. Publ. 45. 80pp.
- HUGIE, R.D. 1982. Black bear ecology and management in the northern conifer-deciduous forest of Maine. Ph.D. Thesis, Univ. Montana, Missoula. 203pp.
- JONKEL, C.J., AND I. MCT. COWAN. 1971. The black bear in the spruce-fir forest. *Wildl. Monogr.* 27. 57pp.
- KOLENOSKY, G.B. 1990. Reproductive biology of black bears in east-central Ontario. *Int. Assoc. Bear Res. and Manage.* 8:385-392.
- LECOUNT, A.L. 1980. Some aspects of black bear ecology in the Arizona chaparral. *Int. Assoc. Bear Res. and Manage.* 3:175-179.
- \_\_\_\_\_. 1982. Characteristics of a central Arizona black bear population. *J. Wildl. Manage.* 46:861-868.
- \_\_\_\_\_. 1987. Causes of black bear cub mortality. *Int. Assoc. Bear Res. and Manage.* 7:75-82.
- MILLER, S.D. 1985. An observation of inter- and intra-specific aggression involving brown bear, black bear, and moose in southcentral Alaska. *J. Mamm.* 66:805-806.
- \_\_\_\_\_. 1987. Susitna Hydroelectric Project Final Report, Big Game Studies, Vol. VI Black and Brown Bear. Alaska Dept. of Fish and Game and Alaska Power Authority. 276pp.
- \_\_\_\_\_. 1990. Population management of bears in North America. *Int. Assoc. Bear Res. and Manage.* 8:357-374.
- \_\_\_\_\_. 1991. Impact of increased bear hunting on survivorship of young bears. *Wildl. Soc. Bull.* 18:462-467.
- \_\_\_\_\_. 1992. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's Game Management Unit 13. Alaska Dep. Fish and Game, Federal Aid in Wildlife Restoration, Research Progress Report on Project W-23-4, Study 4.21. 56pp.
- \_\_\_\_\_. 1993. Development and improvement of bear management techniques and procedures in south-central Alaska. Alaska Dep. Fish and Game, Federal Aid in Wildlife Restoration, Research Progress Report on Project W-24-1, Study 4.24. In press.
- \_\_\_\_\_, E.F. BECKER, AND W.B. BALLARD. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. *Int. Assoc. Bear Res. and Manage.* 7:23-35.
- \_\_\_\_\_, AND D.C. MCALLISTER. 1982. Susitna Hydroelectric Project. Phase I Final Report. Vol. VI Black and Brown Bear. Alaska Dept. of Fish and Game and Alaska Power Authority. 233pp.
- POLLOCK, K.H., S.R. WITERSTEIN, AND C.M. BUNCK. 1989. Survival analysis in telemetry studies: the staggered entry design. *J. Wildl. Manage.* 53:7-15.
- REYNOLDS, D.G., AND J.J. BEECHAM. 1980. Home range activities and reproduction of black bears in west-central Idaho. *Int. Assoc. Bear Res. and Manage.* 3:181-190.
- ROGERS, L.L. 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. *Trans. North Am. Wildl. and Nat. Resour. Conf.* 41:431-438.
- \_\_\_\_\_. 1983. Effects of food supply, predation, cannibalism, parasites, and other health problems on black bear populations. Pages 194-211 in F. Bunnell, D.S. Eastmann, and J.M. Peak, eds. *Symp. Nat. Regulation of Wildl. Popul. For. Wildl. and Range Exp. Stn. Proc.* 14. Univ. Idaho, Moscow. 225pp.
- \_\_\_\_\_. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. *Wildl. Monogr.* 97. 72pp.
- SCHWARTZ, C.C., S.D. MILLER, AND A.W. FRANZMANN. 1987. Denning ecology of three black bear populations in Alaska. *Int. Assoc. Bear Res. and Manage.* 7:281-292.
- \_\_\_\_\_, AND A.W. FRANZMANN. 1991. Interrelationships of black bears to moose and forest succession in the northern coniferous forest. *Wildl. Monogr.* 113. 58pp.
- TAYLOR, M., J.S. CARLEY, AND F.L. BUNNELL. 1987. Correct and incorrect use of recruitment rates for marine mammals. *Marine Mammal Sci.* 32:171-187.