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REPRODUCTIVE BIOLOGY OF BLACK BEARS IN EAST-CENTRAL ONTARIO

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Abstract: The reproductive characteristics of 241 female black bears (*Ursus americanus*) ≥ 3 -years-old were examined in east-central Ontario from 1969-1980. During the 12-year period, the percentage of adult females reproducing each year ranged from 13-58 and averaged 38. Litter sizes ranged from 1 to 4 and averaged 1.9 from summer captures and 2.5 from den examinations. Size of litters was positively correlated with both age of the female ($P < 0.009$) and weight the previous fall ($P < 0.001$) ($N = 28$). Fall weights of 20 adult females that produced cubs the following year averaged 97 kg compared to an average of 70 kg for 14 females that did not produce cubs. Weights of 16 of 20 of the former exceeded 80 kg whereas only 4 of 14 of the latter group were that heavy. Females produced their first litters at ages 5-8; the mean age of first reproduction was 6. Age-specific natality rates for females aged 5-18 ranged from 0.36 to 1.50. Females aged 5-7 produced an average of 0.6 cubs/year and females aged 8-18 an average of 1.2 ($P < 0.01$). Based on 4-8 consecutive years of breeding history, 14 of 15 bears had a 2-year breeding cycle. The male-to-female ratio of cubs produced was 113:100 ($N = 96$). Of the 68 different adult females checked during the study, 59% produced at least one litter of cubs. However 17 of the 68 bears produced 66% of all litters. Characteristics common to the most productive females were longevity, large size, possession of a home range and low vulnerability to hunters. Because a successful female had a high probability of being successful again, the protection of females with young would be a desired management strategy in heavily hunted populations or populations occupying marginal or fragmented patches of habitat.

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Black bears are a classic example of a K-selected species (MacArthur and Wilson 1967) because of their extended life span, low reproductive rate and high parental investment (Graber 1981). Rates of reproduction are among the lowest of any land mammal in North America (Jonkel and Cowan 1971). Productivity (number of young born/year) of a black bear population appears largely density independent and is a function of habitat quality and the number of adult females in the population (Beecham 1980). Because of the species' ecological flexibility, life history parameters are often not interchangeable from one area to another (Beecham 1983). Thus, managers require local data to formulate biologically sound management programs. An understanding of reproductive rates is considered fundamental for management (Herrero 1978). That knowledge becomes increasingly more important as hunting pressure and other mortality factors increase (Beecham 1980).

Objectives of this paper were to define and assess the reproductive characteristics of a black bear population in the conifer-deciduous forests of east-central Ontario and determine the factors relating to annual variations in cub production and survival.

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STUDY AREA

The primary study area of 233 km² is situated between Lake Nipissing and the Ottawa River in east-central Ontario at 46°45' North latitude and 79°20' West longitude (Fig. 1). Underlain by the Canadian Shield, the area

is characterized by exposed outcrops of granites, gneisses and basalts interspersed with sections overlain by glacial and lacustrine deposits (Boissonneau 1968). Much of the western portion is composed of sandy or silty till of low relief: the eastern section varies from gentle undulating and interlobate moraines to precipitous cliffs > 30 m. Soils are shallow and consist largely of a mixture of sand, gravel and boulders. Approximately 11% of the study area consists of small, deep, clear lakes (Kolenosky 1986).

Situated within the Great Lakes-St. Lawrence Forest Region (Rowe 1972), the area represents an ecotone between the boreal forest to the north and the deciduous forest further south. The complex interspersed of deciduous and coniferous trees ranging in age from 0-70 years has produced a diverse habitat highly suitable for bears (Yodzis and Kolenosky 1986).

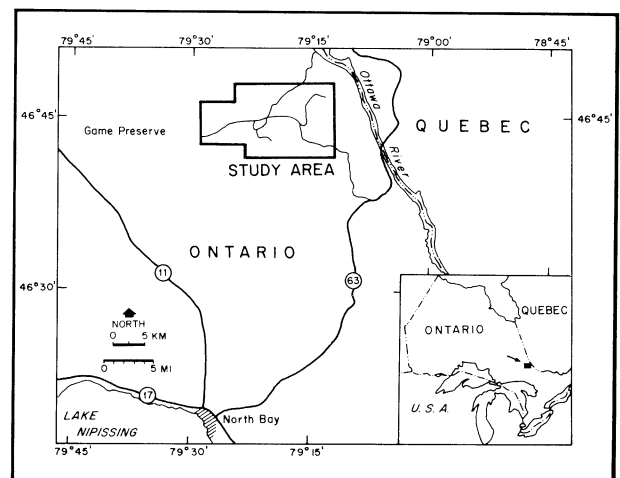


Fig. 1. Location of North Bay study area.

The climate of the area is humid continental (Anon., Atlas of Canada 1957) with cool summers and no dry season. Mean annual temperatures during January and July for North Bay, approximately 40 km south, were -12.8 and 18.3 C, respectively. Mean annual snowfall was 284 cm and average total precipitation 98.8 cm. Approximately 188 days are frost-free each year (Ann. Meteorol. Summary, North Bay Airport 1978).

METHODS

Techniques of capture, marking, and age determination were outlined by Kolenosky (1986), Yodzis and Kolenosky (1986), and Kolenosky and Strathearn (1987). During the first 5 years (1969-73), both baiting and trapping operated on a 10-day open, 4-day closed cycle. From 1974 to 1980, both bait lines and trap lines were run continuously once started. Trapping extended from late May to early September each year. Commencing in 1970, adults were fitted with radio collars (Voigt and Lotimer 1981) and tracked to den sites (Kolenosky and Strathearn 1987).

Vulval swelling was used as an indicator of estrus (Jonkel and Cowan 1971). I derived reproductive rates by multiplying the percentage of captured females lactating by the mean litter size for specific age classes (Stirling et al. 1980). Lactation rates were based on examination of females in dens during spring (1977-80), captures of females with cubs, and females classified as lactating even if cubs were not sighted or found. Litter sizes were determined by counting cubs in dens (Kolenosky and Strathearn 1987), and capturing cubs during the summer field season. In 4 instances when only 1 cub of a litter was captured, other cubs sighted at the site were considered to be part of that litter.

I used chi-square to compare survival of cubs taken at different ages and to compare lactation rates of adult females during the first and latter halves of the study period. To compare fall (August-November) weights of females that produced versus those that did not produce a litter the following year, and to compare lactation rates of different age classes I used *t*-tests. Correlation and linear regression were used to determine relationships between litter sizes versus age and weight of females, annual cub production versus number of adult females, and cub production of specific year classes versus bear years contributed by females ≥ 5 . Statistical tests followed Zar (1974).

RESULTS

During 1969-80 I examined 241 female black bears ≥ 3 -years-old; 182 were ≥ 5 -years-old. Based on vulval

swelling, the breeding season extended from 29 May to 25 August. In most areas females come into heat during early June and remain in heat until they are mated or the ovaries regress (Erickson et al. 1964); that period usually lasts less than 5 days (Rogers 1987). The peak breeding period observed in this study (90% during 10 June-20 July) was similar to that of other North American black bear populations (Rausch 1961, Jonkel and Cowan 1971, Poelker and Hartwell 1973, Kohn 1982, Rogers 1987).

Changes in Female Population

During the 12-year study period, the number of adult females estimated to be present on the study area each year increased from 12 in 1969 to 36 in 1975 and then declined to 18 in 1980 (Table 1). Yearly estimates were based on females captured, radio tracked or assumed to be on the study area for that year if captured both before and after that year. Although a slight change in trapping strategy after 1973 may have contributed to some of the estimated increase, other signs indicated more bears between 1974 and 1978 than during the earlier and later years. These included more sightings of free-ranging bears including cubs and more evidence of other activities such as feeding, tracks, and scats. Reduction in numbers during the final 2 years was attributed to a marked increase in hunting pressure (Kolenosky 1986).

Along with the increase in numbers during the middle years of the study was a continuing increase in mean age.

Table 1. Mean ages of female black bears ≥ 4 and percentage ≥ 8 estimated to be on the study area each year, 1969-80, North Bay Study Area.

Year	Estimated number ^a	\bar{x} age	Percentage ≥ 8	Maximum age
1969	12	5.0	0	6
1970	10	5.7	0	7
1971	18	5.7	11	8
1972	17	6.6	29	11
1973	22	6.7	45	12
1974	28	6.9	43	12
1975	36	7.3	47	13
1976	33	8.3	52	14
1977	29	8.6	59	15
1978	28	8.5	61	16
1979	27	9.1	59	23
1980	18	10.2	61	18

^a Females captured or radio tracked that year or assumed to be on the study area for that year if captured both before and after that year.

From 1969 to 1980, the mean age of adult females more than doubled, from 5.0 to 10.2. The percentage of females ≥ 8 increased from 0% during the first 2 years to an average of 60% during the final 4 years. Maximum age of any individual increased from 6 in 1969 to 18 in 1980. A 23-year-old female was captured in 1979 but since she was captured only once compared to 14-16 captures for some females, and there were no captures of females between the ages of 19-22, she was not considered a part of the continuing progression of aging females.

The increase in mean age was mainly due to the longevity of individual females. Females present as 4- to 6-year-olds in 1969 were the same individuals present as 14- to 16-year-olds 10 years later. The greater survival of established adults, especially females, has been well documented in ursid populations (Craighead et al. 1969, Jonkel and Cowan 1971, Bunnell and Tait 1981, Rogers 1987). The increase in number of mature females during the middle years of the study was probably due to immigration (Yodzis and Kolenosky 1986). That interpretation was based on the finding that the 1969- and 1970-year classes ranked first and third in importance based on the number of different individuals captured, bear years contributed (1 bear year = 1 bear captured at least once in a year) and total cub production. Most of the individuals in those 2 year classes were first captured as 3- to 5-year-olds. If they had been present as cubs, yearlings or 2-year-olds they should have been captured or sighted as all age classes, including the three youngest age groups, were readily captured and often sighted during later years.

Minimum Breeding Age

I considered 4 as the minimum breeding age because no female produced a litter before the age of 5. Of 18 litters for which data were considered adequate to confirm first litters, 8 were 5-years-old, 9 were 6-years-old and 1 was 8-years-old, for an average of 5.7 years. For 6 other females, probable first litters occurred at ages 6 (2), 8 (2), and 9 (2). The average for all of the above females ($N = 24$) was 6.2. The high lactation rate for 6-year-olds (40%) compared to 5-year-olds (24%) and 7-year-olds (12%), indicated that most females produced their first litters at age 6 (Table 2).

Two of the 25 3-year-old females captured were classified as in estrus, but neither had cubs the following year. Of 34 4-year-olds captured, 18% were judged to be in estrus, a value similar to the observed lactation rate for 5-year-olds (24%). As indicated by Jonkel and Cowan (1971) estrus rates derived from captures of wild bears must be regarded as minimal since estrus may occur before or after a specific capture date.

Table 2. Age-specific reproductive rates of female black bears ≥ 3 years, North Bay Study Area, 1969-80.

Age class	N	% Lactating	Litter size	Reproductive rate
3	25	0	0.00	0.000
4	34	0	0.00	0.000
5	34	24	2.00	0.480
6	30	40	2.11	0.844
7	17	12	3.00	0.360
8	17	41	2.60	1.006
9	19	58	2.33	1.351
10	16	44	2.40	1.056
11	13	54	2.00	1.080
12	10	60	2.20	1.320
13-18	23	35	3.17	1.110

Lactation Rates

The percentage of captured females ≥ 5 years lactating each year between 1969 and 1980 ranged from 13 to 58 and averaged 38 (Table 3). The mean lactation rate during the 1975-80 period (42%) was 56% greater than during the 1969-74 period (27%). Differences approached significance ($\chi^2 = 3.7$, d.f. = 1, $P > 0.06$). Synchronization of cub production observed in some sections of black bear range in North America was not evident in my study.

Within age classes, lactation rates ranged from 12% for 7-year-olds to 60% for 12-year-olds (Table 2). Lactation rates for females aged 8-12 (48%) were greater than for females aged 5-7 (27%) ($t = 7.241$, d.f. = 1, $P > 0.006$). Rates for females ≥ 13 -years-old (35%) were

Table 3. Percentage of female black bears ≥ 5 lactating each year, North Bay Study Area, 1969-80.

Year	N Captured	N Lactating	% Lactating
1969	8	1	13
1970	6	2	33
1971	8	2	25
1972	6	3	50
1973	9	3	33
1974	15	3	20
1975	25	9	36
1976	23	6	26
1977	24	14	58
1978	20	9	45
1979	20	8	40
1980	18	9	50
Totals	182	69	

not significantly different than those of the other 2 age classes. The oldest female with a litter was a 19-year-old who produced 2 cubs in 1981 after failing to produce cubs for 3 consecutive years when aged 16 to 18. A 23-year-old female was classified as in estrus when captured on 25 August 1979, but we were unable to determine if cubs were produced the following year.

Average Reproductive Cycle

The average reproductive cycle or breeding cycle (Craighead et al. 1974) based on females with 4-8 years of consecutive breeding history was 2.05 ($N = 15$). A cycle started when a female was lactating, or in estrus and known to have produced the following year. If a female was lactating during the first and last year of the cycle, 1 year was added to the series because it was assumed that females normally reproduce only every other year. Of the 15 bears for which data were available for 4 or more consecutive years, 14 (93%) had a 2-year cycle. The one exception was a female monitored for 8 consecutive years that produced 3 litters during the first 6 years and then failed to produce for 2 consecutive years. That resulted in an overall minimum reproductive cycle of 2.7 years. A total of 87 bear years were involved in the above calculations.

Annual Cub Production

Calculated minimum annual cub production on the study area ranged from 2 in 1969 to 28 in 1977 (Table 4). In instances when a lactating female was captured, but her cubs were not found, an assumed litter size of 2.00 was used to derive the probable number of cubs produced. In any specific year 0 to 2 females were in that category.

During the study period, annual cub production was extremely low at the start, increased gradually for the first 7 years, remained relatively stable for the next 4 years and declined slightly during the final year. As expected, there was a direct relationship between annual cub production and the number of females ≥ 5 years on the study area. The derived equation was cubs produced = $2.69 + 1.07(n \text{ females} \geq 5)$ ($r = 0.91$).

First year survival of cubs varied according to sex and age. For 0.2-year-old cubs marked at dens, 6 of 13 females and 11 of 19 males survived to the age of independence (1.5 years). For cubs captured during the summer when at least 0.5-years-old, 20 of 29 females and 34 of 43 males survived to the age of 1.5 years. Although male survival exceeded female survival by 12% in the den sample and 10% in the capture sample, differences were not significant ($P > 0.4$). However, when the

Table 4. Annual cub production based on captures, sightings and unaccompanied lactating females, North Bay Study Area, 1969-80.

Year	Captured	Sighted	Den examination	Lactating ^a females captured	Probable ^b cub production	Total cubs
1969				1	2	2
1970				2	4	4
1971	2			1	2	4
1972	5	1		1	2	8
1973	4	2		1	2	8
1974	5	2		2	4	11
1975	20	2		1	2	24
1976	14					14
1977	15		13			28
1978	12		10			22
1979	4		14	1	2	20
1980	5		8	2	4	17
Totals	86	7	45	12	24	162

^a Females lactating when captured, but cubs not located.

^b Assumed litter size = 2.00

2 sexes within each sample were combined, cub survival of the capture sample was greater than that of the den sample ($\chi^2 = 4.89$, d.f. = 1, $P > 0.03$). Cub survival was based on subsequent den checks of mothers the following spring and on captures of tagged yearlings the following summer. Because not all tagged individuals were likely captured, first year survival estimates represent minimum values.

Litter Size and Sex Ratio

Size of litters ranged from 1 to 4. Average litter size based on summer captures was 1.9 ($N = 46$) and based on den examinations 2.5 ($N = 18$). Differences were significant ($P < 0.001$). Frequency distribution of litter size of the capture sample was 1-10, 2-33, 3-2, 4-1 and of the den sample 1-1, 2-8, 3-8, 4-1. About 80% of the litters consisted of 2 or 3 cubs. I was unable to determine if first litters of individual females were smaller than subsequent litters but average litter size ($\bar{x} = 2.1$) for the youngest reproducing age groups (5-7) was 14% smaller ($P > 0.05$) than the average litter size for females ≥ 8 ($\bar{x} = 2.5$). The ratio of male to female cubs (113:100, $N = 96$) was essentially equal. The above sample included cubs whose ages ranged from 2 to 8 months.

Sizes of litters were positively correlated with both age of the female ($P < 0.009$) and weight the previous fall ($P < 0.001$). The relationship between fall weight of the female and litter size ($r = 0.61$) was stronger than that between female age and litter size ($r = 0.50$).

Our studies supported results of Rogers (1976, 1987) and Elowe (1987) who noted a relationship between minimum weights of females in the fall and successful reproduction the following spring. Weights of 20 adult females that produced cubs the following year ranged from 59 to 130 kg and averaged 97 ± 18 . Weights of 14 females that did not produce cubs the following year ranged from 45 to 134 kg and averaged 70 ± 26 . Differences were significant ($t = 3.59$, d.f. = 32, $P < 0.002$). Of the females that produced cubs the following year, 16 of 20 (80%) weighed more than 80 kg whereas only 4 of 14 (29%) that did not produce cubs were that heavy in the fall.

Reproductive Rates

Age-specific reproductive rates for female black bears ≥ 5 years ranged from 0.360 for 7-year-olds to 1.351 for 9-year-olds and averaged 0.900 for all females aged 5-18 (Table 2). Rates for all age classes ≥ 8 were greater than 1.000. Females aged 8-18 produced twice as many cubs (1.2) as females aged 5-7 (0.6). Differences were significant ($P < 0.01$), a result of both a larger mean litter size (2.48 vs 2.14) and a higher lactation rate (47 vs 27%) for the older age classes.

Importance of Specific Year Classes

Examination of our data indicated significant differences in importance of specific year classes. To assess importance I compared year classes on the basis of total numbers, bear years contributed, litter production, and calculated cub production (Table 5). Because I used cub production as one of the parameters and bears had to be at least 5-years-old before they produced a litter, only year classes up to 1975 could be used. A bear year refers to an individual bear that was captured at least once during any year. Cub production was derived by multiplying mean litter size X minimum number of litters produced. Year classes were arranged according to cub production with the most productive year class ranked first.

During the 12-year period, an average of 9.9 cubs was produced by the 16 year classes that comprised the sample (Table 5). However production by individual year classes differed markedly and ranged from 27.5 to 0. The 4 most productive year classes produced 60% of all cubs and the 8 most productive 83%. The 3 least productive contributed only 3%.

Cub production by the different year classes was only very weakly related to mean litter size ($r = 0.46$), or to the number of different females in a year class ($r = 0.47$).

Table 5. Reproductive performance of specific year classes of female black bears captured on North Bay Study Area, 1969-80.

Year class	Number different bears	Bear years contributed by females ≥ 5	Minimum number of litters	Litter size		Cub production
				\bar{x}	<i>N</i>	
1969	12	30	11	2.5	11	27.5
1964	6	26	10	2.7	3	27.0
1970	9	22	8	2.7	6	21.6
1965	6	18	7	2.6	5	18.2
1966	8	18	7	1.7	3	11.9
1962	1	8	3	3.0	2	9.0
1967	7	12	4	2.0	4	8.0
1963	4	9	3	2.5	2	7.5
1973	7	6	3	2.5	2	7.5
1975	10	3	3	2.0	1	6.0
1971	5	7	4	1.7	3	5.1
1968	5	8	2	2.5	2	5.0
1961	1	2	1	2.0	1	2.0
1974	10	5	1	—	—	2.0
1956	1	1	0	—	—	0.0
1972	5	0	0	—	—	0.0
Totals	97		67			158.0

However, cub production was more strongly related to the number of females ≥ 5 ($r = 0.72$) and very strongly correlated with the number of bear years contributed by females ≥ 5 ($r = 0.96$). The above relationships indicate that longevity of individual reproducing adult females is probably as important as a large number of females of reproductive age. For instance, if we compare 1965 and 1968, the number of different females in each age class was similar (6 in 1965, 5 in 1968). In the 1965 age group, 5 of 6 were ≥ 5 compared to 4 of 5 in the 1968 year class. However, the 5 females in the 1965 year class produced a minimum of 18 cubs, whereas the 4 in the 1968 year group produced only 5. Differences were mainly due to 2 females in the 1965 age group, 1 of which produced 7 cubs and the other 6. In the 1968 year class, only 2 of the 4 adults present produced a single litter each. A single female born in 1962 remained on the area for 8 consecutive years from 1973-80 and produced a minimum of 9 cubs during that time. The 1969 year class was so productive, primarily because 2 females that were on the area for a total of 14 years produced a total of 15 cubs during that time. Those 2 females contributed 55% of the total production of that year class. The remaining 45% was contributed by 7 other adult females that were present from 1 to 4 years.

Overall, 40 of the 68 different females ≥ 5 produced at least 1 litter of cubs. However, 17 females produced 66% of all litters attesting to the extremely significant contribution of a relatively small number of individuals.

DISCUSSION

Rates of reproduction in a black bear population are affected by age at first breeding, litter size, litter frequency and cub survival. Regional and yearly variations in reproductive rates are largely attributed to differences in diet and nutrition (Spencer 1955, Jonkel and Cowan 1971, Rogers 1976, Beecham 1980, Reynolds and Beecham 1980). Bunnell and Tait (1981) concluded that eastern populations were generally more productive than their western counterparts because of the greater abundance of energy-rich mast and berries. The extremely high reproductive rates of black bears in Pennsylvania were believed to be due to the abundance of natural and human supplied foods (Alt 1981, pers. commun.). In Montana lack of cub production for 3 consecutive years was directly correlated with failure of the huckleberry (*Vaccinium* sp.) crop, a major source of food (Jonkel and Cowan 1971). Rogers (1987) in northeastern Minnesota indicated that crop failures were common and reduced the reproductive rate to less than half the biological potential. In Maine, bears in an area with a superior food base were heavier, bred at an earlier age and produced larger litters than bears occupying an area with poorer food resources (Hugie 1982).

The existence of a latitudinal gradient in black bear minimum breeding age and reproductive rate related to nutrition has been suggested by Reynolds and Beecham (1980). Rausch (1961) in Alaska suggested that the age at which females become sexually mature differs with latitude as a consequence of different growth rates in different geographical regions. The reproductive parameters observed in our area suggest the existence of a latitudinal as well as a longitudinal gradient.

Although sizes of litters in Ontario bears were similar to those of other eastern populations the ages at which females first produced young were not. With a mean age of approximately 6 at first reproduction, females in Ontario reached maturity at about the same age as a western population in Montana (Jonkel and Cowan 1971), but 1 to 2 years later than most eastern populations (Erickson et al. 1964, Sauer 1975, Willey 1978, Alt 1981, Hugie 1982, Kohn 1982, Elowe 1987). In north-central Minnesota, ages at first litter production varied from 3 to 6 (Garshelis et al. 1987) and in northeastern Minnesota from 4 to 8 (Rogers 1987). In the latter area, females with access to garbage produced first litters 1 to 2 years earlier

than individuals lacking supplementary food.

Delays in attaining sexual maturity may be a function of the higher altitude and latitude of the Montana and Ontario study areas, respectively. The locations of both result in a shorter positive foraging period, which would inhibit growth rates and extend the period of development and maturation. The delay in sexual maturation has important management implications because it reduces reproductive potential and hence, allowable harvest levels. Additionally, once a population is overharvested, recovery will be more prolonged (Hilton 1981).

References on duration of breeding cycles for individual female black bears are scarce because of the lengthy studies required for their determination. The average cycle of 2.05 years recorded in our area was slightly shorter than average cycle lengths in northeastern Minnesota (2.28) (Rogers 1987) and Yosemite National Park, California (2.80) (Graber 1981). Although cycles of 2-3 years are the norm, reports of breeding in 2 consecutive years or failing to breed for 2 or more years are not uncommon. In Pennsylvania, 4 of 5 females that lost their litters bred the same year (Alt 1981). The 1 female that did not breed lost her cubs in September after the breeding season. In Arizona, a few females produced litters during consecutive years without loss of cubs (Le Count 1983). In Wisconsin, 31% of adult females captured 2 or more consecutive years did not breed for 2 years in a row and 8% skipped at least 3 years (Kohn 1982). In Montana, Jonkel and Cowan (1971) observed several females that did not have litters for 3 consecutive years.

The percentage of adult females with a litter was highly variable from year to year. Potentially, all females as old, or older than the minimum breeding age could produce a litter every other year. In my area, variations in annual cub production were a function of the numbers, ages, and weights of adult females present. During the first half of the study period, especially during the first 4 years, production was so low because there were so few females of reproductive age and those present failed to gain adequate weight for successful reproduction (Rogers 1976). During the latter years, supplementary energy derived from meat scraps used as bait by the research crew and a local outfitter who catered to bear hunters from early May to 15 June may have contributed to elevated reproductive rates. Between 1969-74, the number of females ≤ 4 estimated to be on the study area ranged from 10 to 28 compared to 18 to 36 during 1975-80. Mean ages, which ranged from 5.0 to 6.9 during the early period, increased from 7.1 to 10.2 during the later period. Maximum ages increased from 6-12 to 13-23. Fall weights ranged from 45-75 kg during 1969-74 and from

45-134 kg during 1975-80. Thus none ($N = 10$) of the females in 1969-74 had attained the minimum fall weight of 80 kg required for successful reproduction whereas 64% ($N = 33$) of those taken in 1975-80 exceeded that value.

First year survival of cubs varies yearly and geographically. Survival is often influenced by physical condition of the female, litter size, experience of the female and age of cubs when marked. Elowe (1987) felt that maximum survival of cubs was linked to some nutritional threshold in females. In Massachusetts, first year survival of female cubs was double that of male cubs (80 vs 38%) (Elowe 1987). The overall mean of 59% in Massachusetts was slightly greater than Ontario means of 53% and 75% for den captures and summer captures, respectively. Differences in survival rates of the 2 Ontario samples may reflect the mortality that occurs between 2.5 and 5.0-8.0 months. In north-central Minnesota, first year survival of cubs was 84% (Garshelis et al. 1987) and in northeastern Minnesota 59-88% depending upon yearly food supplies (Rogers 1987). In Pennsylvania, cub survival was inversely related to litter size and ranged from 0-100% (Alt 1981). In Montana, survival of cubs from 0.5-1.5 years was 87% (Jonkel and Cowan 1971).

Most populations are managed on the assumption that individuals within a population are interchangeable. Thus, the basic requirements for management are a knowledge of total numbers, sex and age ratios, birth rate and death rate. However, populations are composed of individuals and individuals differ (Wellington 1957). The occurrence of dominant year classes has long been recognized in fish populations (Ricker 1975) but has received less attention in mammals where annual production is relatively more even. One difference has been the observed association between social status and increased fecundity with high ranking individuals being the most productive (Rutberg 1986). Clutton-Brock et al. (1983) showed that some red deer (*Cervus elaphus*) hinds were consistently successful breeders whereas others were consistently unsuccessful. In grizzly bears (*U. arctos*), the reproductive output of females varied among individuals (Craighead et al. 1969). Rogers (1987) commented on an adult female black bear whose reproductive success was above average in both birth rate and cub survival. He attributed her superior output to her greater knowledge of local food sources.

The presence of some females in my area that were repeatedly successful whereas others were not raises intriguing questions about differences in individuals. A complex array of interacting physical and environmental

factors probably contributed to the greater success of certain females. A number of characteristics that were common to the most successful females included the following:

1. Possession of an established home range — Requirements for survival and reproduction are directly linked to the size and quality of a females' home range. Rogers (1987: 42, 51, 55) showed that exclusive feeding areas may provide reproductive advantages to dominant females. In my area, resident adult females produced an average of 0.85 cubs/year compared to 0.17 for those classified as transients.
2. Physical size — Generally, the most successful females were above average size and weight, with the proportion of females with litters higher for the larger females. Physical size was also age related as most females continued to gain weight up to 8-years-old.
3. Longevity — Obviously, to be successful, a female must stay alive. Longevity is at least partly a function of habitat characteristics within the female's home range, the female's physical alertness and perhaps genetic inheritance and early training. The presence of adequate food and escape cover within an individual's home range would be important ingredients.
4. Low vulnerability — Although closely related to longevity, it differs in that longevity is usually associated with natural phenomena that might affect life span whereas vulnerability is related to human-caused forces. The most successful females avoided hunters for up to 8-10 years despite a spring and fall hunting season each year. Most adult resident females did not become vulnerable until the final few years of the study when hunting pressure had increased 800% over earlier years (Kolenosky 1986).

Social factors are undoubtedly important in determining locations and apportioning sizes of ranges of individual bears which are important for reproduction and survival. Although females in our area were slow to mature, reproductive rates were comparable to other populations once reproduction started. Because maximum reproductive levels were not reached until females were at least 8-years-old, the presence of older individuals was very important for the maintenance of the population. Because a female with cubs indicated she was a successful breeder with a higher probability of future reproductions, the protection of family groups would be a desired management strategy in heavily hunted populations or populations occupying marginal or fragmented patches of habitat. The complete protection of all females would be even more desirable, but realization of such a strategy

would be difficult because of problems in identifying the sex of free-ranging bears.

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