

# BODY SIZE AND BLOOD CHARACTERISTICS AS INDICATORS OF CONDITION AND REPRODUCTIVE PERFORMANCE IN BLACK BEARS

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*Abstract:* We examined relationships between reproductive performance of female Minnesota black bears (*Ursus americanus*) and various potential indicators of nutritional condition during late hibernation. Litter size ( $n = 101$  litters) was influenced more by litter order (first or subsequent) than by maternal condition, except perhaps in very large females. An increased proportion of male cub births corresponded with increased maternal weight and serum alkaline phosphatase (ALKP) and decreased serum creatinine (CR). Weight and growth of cubs and yearlings were closely related to mother's size; they also correlated positively with maternal ALKP, and negatively with serum total protein (TP), and mean corpuscular volume (MCV). Cub survival was affected only when mother's weight 2 months postpartum was below about 65 kg. No juvenile females (2-8 years old) weighing <41 kg in March produced their first cubs the following spring, but 57% of those above this threshold weight produced cubs. Litter frequency and yearling recruitment were unrelated to maternal condition. Life history parameters of black bears appear to respond to declining nutrition in the following sequence: (1) litter size declines, then stabilizes across a broad range of maternal weights; (2) age of first reproduction increases; (3) juvenile survival decreases; (4) first-year cub survival decreases; and (5) litter frequency decreases. Better definition of these relationships, particularly at nutritional extremes, will likely require collaborative efforts of researchers studying diverse populations.

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Size and condition of adult female black bears are known to influence reproductive performance, but relationships between condition and individual reproductive parameters have not been well defined. Nutritional condition of females has been variously reported to correspond with their age of first reproduction, litter size, interval between litters, and growth and survival of cubs (Beecham 1980, Rogers 1987, Alt 1989, Eiler et al. 1989, Elowe and Dodge 1989, Kolenosky 1990, Stringham 1990). In most studies, differences in maternal condition have been inferred from subjective assessments of food supply (Rogers 1976, 1987; Eiler et al. 1989, Elowe and Dodge 1989) or habitat quality (Jonkel and Cowan 1971, Beecham 1980, Reynolds and Beecham 1980). In only a few cases have reproductive parameters been specifically linked to physical attributes of female bears, such as mean weights within populations (Alt 1989, Stringham 1990) or weights of individual females (Rogers 1976, 1987; Alt 1982, 1989). Results of these studies have not always been corroborative.

Body size may not be the only useful index of nutritional condition. Metabolic indicators have shown promise for other species (Franzmann and LeResche 1978, Seal et al. 1978, Warren et al. 1982, Corn and Warren 1985, DelGiudice et al. 1987a, Hawley 1987), and recent studies have suggested that they may be useful for bears as well (Schroeder 1987, Franzmann and Schwartz 1988, Hellgren et al. 1989, DelGiudice et al. 1991). Serum chemistry and hematology of bears vary not only with season and reproductive state (Erickson and Youatt 1961, Seal et al. 1967, Halloran

and Pearson 1972, Pearson and Halloran 1972, Franzmann and Schwartz 1988, Hellgren et al. 1990), but also with body size (Schroeder 1987, Hellgren et al. 1989, 1993) and annual fluctuations in food supply (DelGiudice et al. 1991, Hellgren et al. 1993). Elowe and Dodge (1989) attempted to relate blood chemistry directly to reproductive performance of females, but found no correlations.

Our purpose was to examine the relationship between several potential physical and metabolic indicators of nutritional condition and the reproductive output of individual females. Bears in our study area displayed a fairly wide range of reproductive values and thus could serve well for testing these relationships.

We focused our examination on hibernating females in late winter for 2 reasons. First, serum concentrations of many blood components are known to fluctuate in response to diet and/or capture stress (Franzmann and LeResche 1978, Seal 1978, Seal and Hoskinson 1978, Brannon 1985a,b). In hibernating bears, differences due to underlying nutritional condition would not be confounded by recently ingested food, and capture stress would be minimized. However, some nutritional effects might be masked by physiologic changes due to the hibernation state itself. Second, the period following emergence from dens carries particularly high energetic costs for bears, as the green vegetation bears generally rely on in early spring is lower in digestible energy than summer and fall foods (Pritchard and Robbins 1990). Indeed, most natural mortality in cubs and juveniles typically occurs within 3 months after leaving the den (Rogers 1987, Elowe

and Dodge 1989, Beck 1991, Schwartz and Franzmann 1991). Furthermore, this period is immediately followed by the breeding season, during which time a female's condition may influence her fertility. Thus, late-winter condition potentially influences several aspects of growth and reproduction, including milk production in lactating females (hence cub growth rates), survival of young bears, likelihood of juveniles to achieve puberty, and likelihood of nonlactating females to breed successfully.

This project was supported by the Forest Wildlife Populations and Research Unit of the Minnesota Department of Natural Resources as part of an ongoing study of the population dynamics of black bears in north-central Minnesota. We wish to acknowledge P. Coy for her valuable contributions to all aspects of the fieldwork; she also provided all interpretations of cementum annuli for age estimation and reconstruction of reproductive histories. Many other people assisted with data collection during trapping and at winter dens. K. Kerr performed all blood analyses. G. DelGiudice, E. Hellgren, and 1 anonymous reviewer provided helpful comments on the manuscript.

## STUDY AREA

The study was conducted on the Marcell District of the Chippewa National Forest and the adjoining George Washington State Forest (47°30'N, 93°30'W) in north-central Minnesota, approximately 30 km north of Grand Rapids. The area is >95% forested, with major forest types typical of the transition between the eastern hardwood and northern boreal types. Aspen-dominated forests (*Populus tremuloides* with *Betula papyrifera* and *Abies balsamea*) predominate on the uplands, with lesser amounts of conifer (*Pinus resinosa*, *Pinus strobus*, *Picea glauca*) and hardwoods (*Acer saccharum*, *Tilia americana*, *Quercus rubra*). Lowland forests of black spruce (*Picea mariana*), tamarack (*Larix laricina*), northern white cedar (*Thuja occidentalis*), and black ash (*Fraxinus nigra*) comprise approximately 33% of the forested area.

These forests provide a wide variety of plant foods utilized by bears, including fruits of wild sarsaparilla (*Aralia nudicaulis*), juneberry (*Amelanchier* spp.), blueberry (*Vaccinium* spp.), cherry (*Prunus* spp.), raspberry (*Rubus strigosus*), blackberry (*Rubus allegheniensis*), dogwood (*Cornus* spp.), and *Viburnum* spp. during the summer and early fall. Nuts of hazel (*Corylus* spp.), which is widespread, and oak (*Quercus* spp.), which is spotty in distribution, provide energy-rich fall foods in some years. Upland forests,

especially young stands (10-20 years old), typically produce much more summer food than lowland areas (Noyce and Coy 1990). In spring and early summer, before wild fruits become available, bear foods consist primarily of green vegetation, ants, and white-tailed deer fawns (*Odocoileus virginiana*) (Garshelis et al. 1987).

The mean July temperature at Grand Rapids is 19°C and the January mean is -15°C (Natl. Oceanic and Atmos. Adm. 1990). Annual precipitation averages 67 cm, of which 44 cm fall as rain during May-September.

## METHODS

Bears were trapped and fitted with radio collars during May-July, 1981-89, at which time a first upper premolar was extracted for age estimation from cementum annuli (Willey 1974). Radio-collared bears were tranquilized in their winter dens during February-March, 1982-93, and immobilized with either a mixture of ketamine hydrochloride (11-13 mg/kg) and promazine (0.6-0.7 mg/kg) or tiletamine hydrochloride and zolazepam (Telazol, 3.9-5.3 mg/kg). Bears were then weighed and measured. We collected blood from bears  $\geq 11$  months old weighing  $\geq 11$  kg in all years except 1993. Whole blood was collected in Vacutainer tubes containing EDTA anti-coagulant. Serum was obtained from coagulated blood samples, centrifuged within 12 hours of collection, and stored frozen.

During den visits, cubs and yearlings were counted, sexed, and weighed. Cubs were assumed to have died if they were not present as yearlings in their mothers den. (In this study, no missing cubs have ever subsequently been trapped or recovered in the harvest.) All yearlings were fitted with radio collars and monitored until their death. Age of first reproduction was determined during yearly den checks. For bears with unknown histories, reproductive maturity (pre-, primi-, or multiparity) was based on spacing of cementum annuli (Coy and Garshelis 1992) and nipple characteristics (Garshelis et al. 1989).

We chose 11 functions of body measurements and 9 blood characteristics, most of which had been previously suggested in the literature as potential nutritional indices, to test against reproductive performance. Physical indices included: weight (WT), log of weight (LOGWT), cube root of weight (CRTWT), total length (from nose-tip to tip of tail) (LN), skull length (SK), humerus length (HUM), ratios of WT/LN, WT/SK, CRTWT/LN, and an index (CND) expressing the ratio of body radius to length, based on a cylindrical model of body shape ( $\text{Volume} = \text{LN}\pi r^2$ ;

then substituting WT for volume,  $CND = r/LN = \sqrt{WT/LN\pi}/LN$ .

Serum was analyzed for urea nitrogen (SUN; Wybenga et al. 1971), creatinine (CR; Heinegard and Tiderstrom 1973), total protein (TP; Henry et al. 1957), alkaline phosphatase (ALKP; Sigma units or Bessey-Lowry-Brock units/ml, 37°C; Bessey et al. 1946), total lipids (TLIP; Frings et al. 1972), and cholesterol (CHL; Huang et al. 1961). Red blood cells (RBC) were counted using a Fisher autocytoimeter (No. 6-246V1), and hemoglobin (HGB) (Eilers 1967) and mean corpuscular volume (MCV) were determined. All analyses were performed at the Forest Wildlife Research Lab of the Minnesota Department of Natural Resources, Grand Rapids, Minnesota. Not all analyses were performed on all blood samples.

Bears were classified by reproductive status (juveniles = no cubs produced; lactating females = accompanied by cubs of the year; nonlactating/barren adult females = either accompanied by offspring from a previous year or alone, having lost or separated prematurely from a previous year's litter). Litters from the same female and cubs from the same litter were treated as independent samples, thus ensuring adequate sample sizes to investigate the effects of several variables simultaneously. We also used yearly samples from the same bear as independent samples because it appeared that changes in body size (with age) and/or yearly variations in food supply might have as great an influence on maternal condition (and hence on reproduction) as the effects of individual. However, to guard against potential bias due to repeated sampling of some individuals, we also calculated mean values for individual females and analyzed them with respect to measures of their individual reproductive performance. This, however, obscured the magnitude of year-to-year variation in individuals.

Statistical analyses were performed using the procedures provided in SAS (SAS Institute, Inc., Cary, N.C.). We looked for predictors of reproductive output using both single- and multiple-variable models. As WT, CRTWT, LOGWT, WT/LN, and WT/SK were autocorrelated ( $r^2 \geq 0.95$ ), these were not used simultaneously in multiple-variable models. Logistic regression (Proc. LOGISTIC) was used to test for differences in the response probabilities for variables with a binary response, such as sex of cubs (male or female), survival of cubs (yes or no), and cub production (yes or no). Litter size, an ordered categorical response (1-5) with non-normal distribution, was analyzed using the categorical models procedure (Proc. CATMOD). Regression and analysis of variance

were used to investigate cub and litter weights and across-year measures of recruitment (Proc. REG and GLM).

## RESULTS

### Characteristics of Females in Late Winter

Lactating and nonlactating adult female black bears measured in their dens during February and March were similar in skeletal size, but lactating females weighed more than barren females, and had higher concentrations of SUN and ALKP (Table 1). In contrast, TP, TLIP, and CHL were lower in lactating females, whereas HGB, MCV, RBC, and CR did not differ between the 2 groups. Characteristics of blood in both groups were unrelated to any measures of body size or body proportion, except that in nonlactating females, SUN tended to decrease with increases in body weight ( $r^2 = 0.36$  for SUN vs LOGWT,  $P < 0.0001$ ,  $n = 61$ ).

### Litter Size

Litter size was largely unaffected by maternal body size ( $n = 101$  litters produced by 45 different females). Initial categorical analysis suggested that number of cubs might be positively related to maternal weight 2 months postpartum ( $\chi^2 = 8.32$ , 4 df,  $P = 0.08$ ). However, we found that first litters tended to be smaller than subsequent litters (3 or more cubs in 62% of second litters and 78% of third or subsequent litters, but only 13% of first litters), and in a 2-way categorical analysis, testing the effects of both maternal weight and litter order (first or subsequent) on litter size, only the effect of litter order was significant ( $\chi^2 = 25.7$ , 1 df,  $P < 0.0001$ ). The apparent relationship between litter size and maternal weight, when first and subsequent litters were pooled, resulted because females producing their first litters tended to be smaller ( $\bar{x} = 64.0$  kg,  $n = 29$ ) than multiparous females ( $\bar{x} = 82.4$ ,  $n = 72$ ;  $t = -7.4$ ,  $P < 0.0001$ ) (Table 2).

Likewise, the average size of litters born to individual females was unrelated to their across-year average weight ( $n = 23$ ; females observed through at least 2 litters, not counting first litters)(Fig. 1). Among these females, the only suggestion that maternal weight might influence number of cubs born was a bear that averaged 123 kg 2 months postpartum (23 kg more than any other female in the study) and produced 5, 5, 3, and 3 cubs in 4 consecutive litters. However, the only other female that produced more than 3 cubs (1 litter of 4 cubs and 2 litters of 3 cubs) averaged only 64 kg

**Table 1. Mean values of physical and blood characteristics from adult female black bears during February-March in north-central Minnesota, 1981-93.**

	Reproductive status							
	Nonlactating				Lactating			
	$\bar{x}$	(n)	SE	Range	$\bar{x}$	(n)	SE	Range
Weight (kg)	69.5 <sup>a</sup>	(72)	1.8	(44-111)	77.0 <sup>a</sup>	(104)	1.7	(50-141)
Length (cm)	150.3	(72)	1.1	(131-175)	151.9	(100)	1.0	(139-192)
Skull (cm)	32.8	(72)	0.2	(30-36)	32.7	(101)	0.1	(30-36)
HGB (g/dL)	17.3	(54)	0.2	(13.5-20.4)	17.0	(80)	0.2	(13.4-21)
MCV (fL)	56.9	(30)	0.6	(51-63)	56.8	(38)	0.5	(52-66)
RBC ( $10^6/\mu\text{l}$ )	8.7	(30)	1.3	(71-101)	8.6	(38)	1.3	(65-105)
SUN (mg/dL)	6.9 <sup>a</sup>	(61)	0.5	(1-24)	8.5 <sup>a</sup>	(91)	0.4	(1-20)
CR (mg/dL)	3.1	(63)	0.09	(1.7-4.9)	3.1	(93)	0.06	(2.0-4.7)
TP (g/dL)	7.8 <sup>a</sup>	(49)	0.1	(6.4-10.6)	7.2 <sup>a</sup>	(75)	0.06	(5.8-8.8)
ALKP <sup>b</sup>	2.4 <sup>a</sup>	(54)	0.1	(1-6)	2.9 <sup>a</sup>	(82)	0.1	(1-5)
TLIP (mg/dL)	1,075.0 <sup>a</sup>	(54)	42.2	(571-2263)	778.3 <sup>a</sup>	(82)	21.6	(456-1433)
CHL (mg/dL)	404.7 <sup>a</sup>	(61)	13.7	(210-688)	300.1 <sup>a</sup>	(92)	7.7	(151-522)

<sup>a</sup> Values for lactating and nonlactating females are different at  $P \leq 0.01$  (*t*-test).

<sup>b</sup> Sigma units or Bessey-Lowry-Brock units/ml, 37°C; Bessey et al. 1946.

(69 kg in the 4-cub year), well below the average for a multiparous female. Average postpartum HGB in the same 23 females showed a weak inverse relationship to average litter size ( $r^2 = 0.29$ ,  $P = 0.008$ ).

### Sex of Cubs

Sex of cubs was related to mother's weight and also to litter size. Proportion of males increased with increasing maternal weight, and in litters of 1-3 cubs, decreased with increasing litter size (Table 3) (2-variable logistic regression model;  $\chi^2 = 8.7$ , 2 df,  $P = 0.01$  for the model,  $P = 0.02$  and  $P = 0.03$  for the individual effects of mother's weight and litter size, respectively). Nine of eleven single cubs (82%) were

male, whereas only 52% of cubs in 3-cub litters were male.

Two blood parameters in mothers also appeared related to cub sex ratio. Within litters of the same size, increased ALKP 2 months postpartum corresponded with production of more male-biased litters (Table 4) (2-variable logistic regression;  $\chi^2 = 12.6$ ,  $P = 0.002$  for the model,  $P = 0.03$  and  $P = 0.006$  for the effects of ALKP and litter size, respectively,  $n = 197$ ). Mean CR concentrations (averaged across at least 2 years) in individual mothers during nonlactating years corresponded with a reduced percentage of males in litters previously or subsequently produced (male cubs/total cubs produced in 2 or more litters) (Fig. 2;

**Table 2. Mean litter size of first and subsequent litters born to female black bears of different weights, north-central Minnesota, 1981-93.**

Litter order	Mother's weight (kg) <sup>a</sup>					
	<60	60-69	70-79	80-89	≥90	All
	$\bar{x}$ (n)	$\bar{x}$ (n)	$\bar{x}$ (n)	$\bar{x}$ (n)	$\bar{x}$ (n)	$\bar{x}$ (n)
First	2.1 (10)	1.8 (12)	2.0 (7)			2.0 (29)
Subsequent	2.7 (6)	2.7 (14)	2.6 (12)	2.7 (17)	2.7 (23)	2.7 (72)
Combined	2.3 (16)	2.3 (26)	2.4 (19)	2.7 (17)	2.7 (23)	2.5 (101)

<sup>a</sup> Adult females were weighed in maternal dens between 9 March and 25 March, approximately 2 months postpartum.

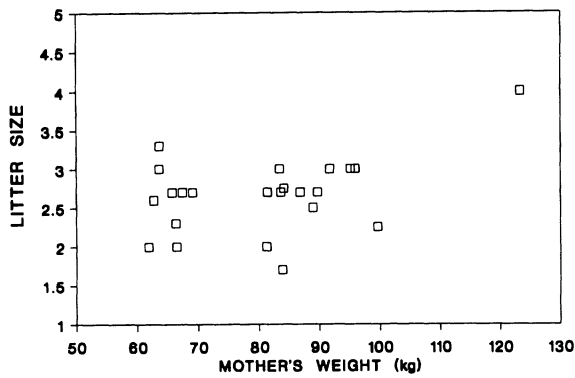


Fig. 1. Relationship between litter size and maternal weight, 2 months postpartum, in black bears, north-central Minnesota, 1981-93. Points represent across-year means for individual females monitored through at least 2 litters, not counting first litters.

$r^2 = 0.48, P = 0.002, n = 17$ .

**Weight and Growth of Cubs**

Mother's weight (2 months postpartum) accounted for 28% of the variation in individual cub weights ( $P < 0.0001, n = 253$ ) and 40% of the variation in total litter weights ( $P < 0.0001, n = 101, \text{Fig. 3}$ ). Log of weight and CRTWT were similarly related to cub weight ( $r^2 = 0.30$  and  $0.28$ , respectively) and litter weight ( $r^2 = 0.40$  for both), but other measurements of body size were not. Cub weight was influenced also by litter size and litter order ( $F = 5.72, \text{df} = 5, P < 0.0005$ ). Cubs from first litters averaged 2.7, 2.4, and 2.0 kg in litters of 1, 2, and 3 cubs, respectively, whereas cubs in subsequent litters were larger, with mean weights of 3.5, 2.8, and 2.5 kg in 1, 2, and 3 cub litters.

No maternal blood parameter was significantly related to either cub or litter weight in single-variable regression models. Multiple regression indicated,

however, that when litter size, litter order, and maternal LOGWT were adjusted for, ALKP (2 months postpartum) was positively related to cub weight, and TP and MCV were inversely related to both cub and litter weights. These relationships were too weak to have predictive utility (Partial  $r^2 = 0.12, 0.16,$  and  $0.17$ , for ALKP, TP, and MCV with cub weight,  $P < 0.0001, n = 82$ ; Partial  $r^2 = 0.42$  and  $0.26$  for TP and MCV with litter weight,  $P \leq 0.002, n = 35$ ). Together, LOGWT, litter size, MCV, and TP accounted for 90% of the variation in litter weights, whereas LOGWT and litter size alone accounted for 82% of the variation.

Mother's weight was also the best predictor of yearling size. Mean WT calculated for individual females in years when they were lactating explained 55% and mean LOGWT explained 63% of the variation in the average weights of their yearlings ( $P \leq 0.0001, n = 32, \text{Fig. 4}$ ). Mean LOGWT calculated for individuals during nonlactating years explained 44% of this variation ( $P \leq 0.0001, n = 34$ ). We failed to find any significant relationships between blood characteristics of lactating females and the size of their yearling offspring. Multiple regression (including LOGWT as a regressor) indicated an inverse relationship between mean CR in nonlactating females and the weight of their yearling offspring, but this relationship was too weak to have practical utility (Partial  $r^2 = 0.24, P = 0.005, n = 32$ ).

**Cub Survival**

Cubs weighing  $< 1.5$  kg at 2 months of age had lower first-year survival than larger cubs ( $\chi^2 = 24.3, 1 \text{ df}, P < 0.0001, n = 197$ ). Only 1 of 6 cubs  $< 1.5$  kg survived, whereas  $\geq 80\%$  survived in each heavier weight class (1.5-1.9, 2.0-2.4, 2.5-2.9, 3.0-3.4,  $> 3.4$  kg;  $n = 15-53$ ). Survival also was related to sex of cubs ( $\chi^2 = 3.7, 1 \text{ df}, P = 0.05$ ); 91% of female cubs, but only 81% of male cubs survived their first summer.

Table 3. Sex ratios of black bear cubs in litters produced by mothers of different weights, north-central Minnesota, 1981-93.

Litter size	Mother's weight (kg) <sup>a</sup>				All weights % M (n)
	<60 % M (n)	60-74 % M (n)	75-89 % M (n)	$\geq 90$ % M (n)	
1 cub		80 (5)	100 (4)	50 (2)	82 (11)
2 cubs	45 (24)	57 (28)	67 (12)	70 (10)	57 (74)
3 cubs	27 (15)	51 (45)	51 (57)	62 (45)	52 (162)
All litters <sup>b</sup>	38 (39)	55 (78)	55 (73)	63 (57)	55 (247)

<sup>a</sup> Adult females were weighed in maternal dens between 9 March and 25 March, approximately 2 months postpartum.

<sup>b</sup> Two litters of 5 cubs and 1 litter of 4 cubs were not included in this table.

**Table 4. Sex ratio (% male) of black bear cubs versus maternal serum concentrations of alkaline phosphatase (ALKP), 2 months postpartum, by litter size, north-central Minnesota, 1981-93.**

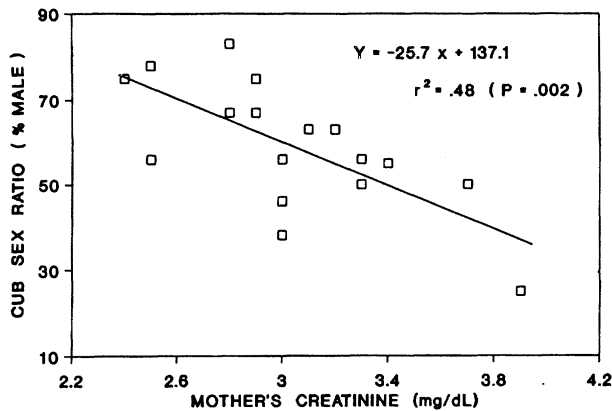
Litter size	Maternal ALKP (units <sup>a</sup> /ml)					Pooled % M (n)
	1.0-1.9 % M (n)	2.0-2.9 % M (n)	3.0-3.9 % M (n)	4.0-4.9 % M (n)	5.0-5.9 % M (n)	
1 cub		100 (2)	100 (5)	100 (1)	50 (2)	90 (10)
2 cubs	67 (6)	50 (14)	64 (22)	88 (8)		64 (50)
3 cubs	0 (3)	45 (42)	48 (54)	63 (35)	67 (3)	50 (137)
Pooled	44 (9)	48 (58)	55 (81)	68 (44)	60 (5)	56 (197)

<sup>a</sup> Sigma units or Bessey-Lowry-Brock units, 37°C; Bessey et al. 1946.

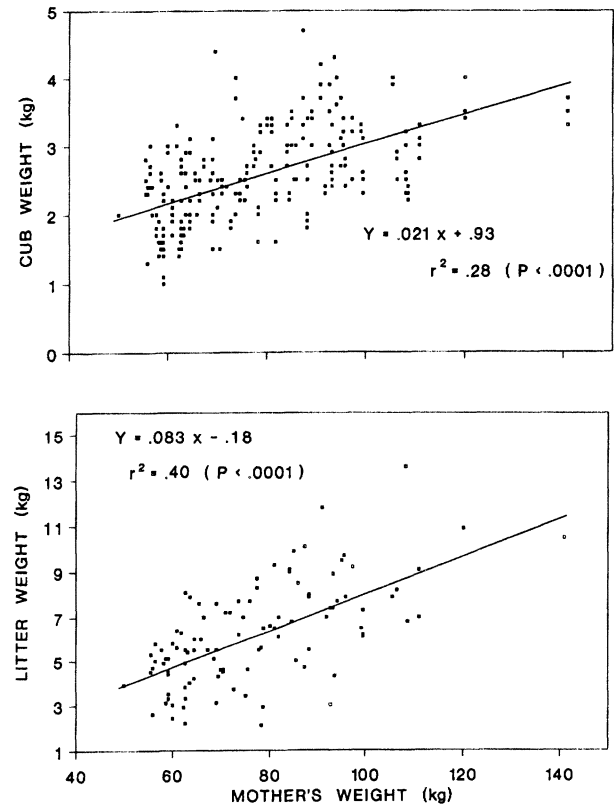
Excluding the 6 cubs that weighed <1.5 kg, the disparity between first-year survival of females (96%) and males (81%) was even larger ( $\chi^2 = 9.9$ , 1 df,  $P = 0.002$ ).

The effect of cub weight on survival appeared to extend into their second and third summers as well ( $\chi^2 = 9.4$ , 5 df,  $P = 0.09$ ). Of 36 yearlings that weighed <2.0 kg as cubs, 4 (11%) died of starvation between March and May of their second year. Additionally, 1 other bear, which weighed 2.2 kg as a cub, died of starvation (complicated by porcupine quills) as a 2-year-old. All 5 of the bears that died of starvation, although above the 1.5 kg threshold for first-year survival, weighed only 5.9-9.8 kg at 14 months of age. There was no starvation mortality among yearlings  $\geq 10$  kg, and all cubs that weighed >2.2 kg at 2 months of age

exceeded the 10 kg weight threshold as yearlings. Only 1 bear that weighed <10 kg at 14 months old survived; she had also been a small cub (2.1 kg) and was the sibling of the female that died as a 2-year-old. Although she survived, she remained the smallest bear for her age in our study, and was the only female that had not produced cubs by the time she was 8 years old.



**Fig. 2. Relationship between March serum creatinine concentrations in hibernating adult female black bears during nonlactating years and sex ratios of cubs they previously or subsequently produced, north-central Minnesota, 1981-93. Creatinine values represent across-year means for individual females monitored through at least 2 reproductive cycles; cub sex ratios were calculated from across-year totals for those females (male cubs/total cubs produced in at least 2 litters.)**



**Fig. 3. Relationship between maternal weight in black bears and weights of cubs (A) and whole litters (B), 2 months postpartum, north-central Minnesota, 1981-93 (n = 253 cubs and n = 101 litters produced by 45 different females).**

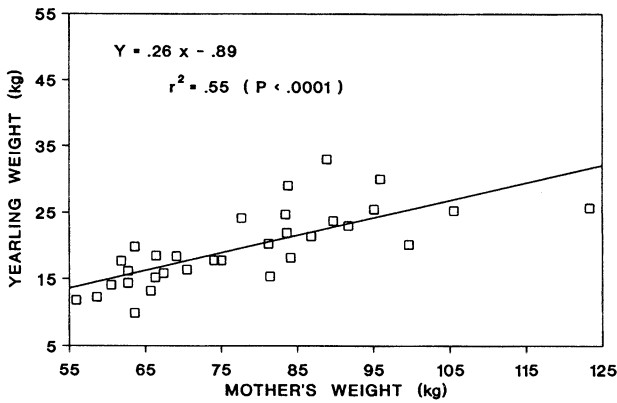


Fig. 4. Relationship between maternal weight in black bears, 2 months postpartum, and weights of yearlings, north-central Minnesota, 1981-93. Points represent across-year means for all individual females that raised cubs to 14 months of age.

Maternal weight influenced survival of offspring in that cubs and yearlings of lightweight mothers were less likely to reach threshold survival weights than those of heavier mothers. Seven of 39 (18%) and 1 of 40 (3%) cubs produced by females weighing < 60 kg and 60-64 kg, respectively, weighed < 1.5 kg at 2 months old, whereas only 1 of 169 cubs produced by females  $\geq 65$  kg failed to attain this weight ( $\chi^2 = 27.5$ , 2 df,  $P < 0.0001$ ). Six of 48 yearlings raised by mothers < 65 kg were below the 10-kg yearling weight threshold, whereas all yearlings raised by mothers  $\geq 65$  kg exceeded this weight ( $\chi^2 = 4.3$ , 1 df,  $P = 0.04$ ).

No measured blood characteristics of mothers in late winter showed any relationship to the survival of their cubs. Because of their poor condition, we did not collect blood from any of the yearling bears that later died of starvation. However, samples obtained at 23 months of age from the 2 females that weighed < 10 kg as yearlings but survived to 2 years showed low protein concentrations relative to other females their age: 6.6 mg/dL in the one that later died (the lowest value recorded) and 6.9 mg/dL in the one that survived but remained very small ( $\bar{x}$  for 2-year-old females = 7.3 mg/dL, SE = 0.09,  $n = 22$ ).

Age of First Reproduction

No juvenile female (2-8 years old) weighing < 41 kg in March produced her first cubs the following winter ( $n = 37$ ). In contrast, 57% of those weighing  $\geq 41$  kg produced litters the next year ( $n = 42$ ). For juveniles  $\geq 41$  kg, further increases in weight did not increase the likelihood of having cubs, but increased WT/LN ratios and a higher CND index did (WT/LN:  $\chi^2 = 9.8$ , 1 df,  $P = 0.002$ ; CND:  $\chi^2 = 7.3$ , 1 df,  $P = 0.007$ ;

$n = 38$ ). Additionally, first-time cub production was related to CR concentrations the previous year ( $\chi^2 = 6.0$ , 1 df,  $P = 0.01$ ,  $n = 27$ ). Only 2 of 9 juveniles with CR levels  $\leq 2.5$  mg/dL produced cubs the next year, whereas 8 of 14 with CR levels of 2.6-3.2 mg/dL, and all 4 females with CR  $\geq 3.3$  mg/dL produced their first litters the next year (Fig. 5). In 2-factor logistic regression models, the effect of CR was most pronounced, and WT/LN was a better predictor than CND ( $\chi^2 = 11.1$ , 2 df,  $P = 0.004$ ,  $n = 26$ ).

Litter Frequency

All but 4 of 64 pairs of consecutive litters occurred  $\leq 2$  years apart. In 3 of the 4 cases where cubs were not produced at the expected 2-year interval, the females denned with their offspring an additional year. In at least 2 cases, the females had rejoined their previously estranged yearlings after the breeding season. We discerned nothing in the weights or blood profiles of the females that skipped a reproductive year, either during the winters prior to expected breeding or during the winters of failed cub production, that distinguished them from females that reproduced successfully.

Five females lost entire litters prior to the breeding season, resulting in 2 consecutive years of cub production. One additional female lost her litter but was killed before subsequent reproduction could occur. Four of the 6 litters of cubs that died were first litters. Of those 4 litters, 2 consisted of a single cub and 1 of lightweight cubs (< 1.5 kg). Two of the litters were

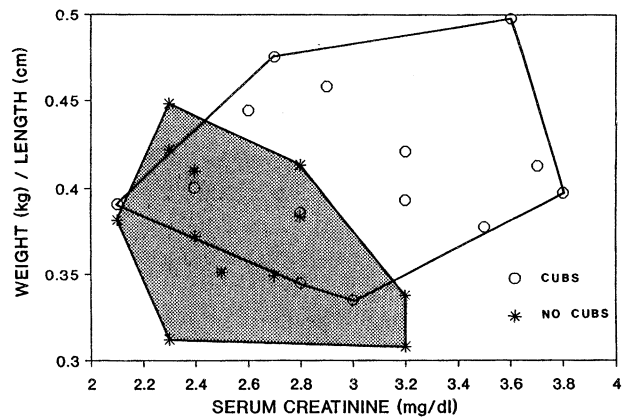


Fig. 5. March serum creatinine concentrations and weight/length ratios of juvenile female black bears that did and did not produce their first cubs the following winter, north-central Minnesota, 1981-93. (Only those weighing  $\geq 41$  kg in March were included, as no females < 41 kg produced cubs the next year.)

produced by multiparous females; 1 was comprised of a single cub and 1 of 3 lightweight cubs. Again there were no apparent differences between the physical or blood characteristics of the females that lost litters and those that successfully raised cubs.

### Recruitment

We examined 3 measures of annual recruitment for individual adult females, using only females monitored through at least 2 litters other than their first: (1) number of cubs produced per year, (2) number of yearlings recruited per year, and (3) total biomass of yearlings recruited per year. Cub recruitment was essentially equivalent to half the mean litter size, as most females produced cubs every other year. Yearling recruitment reflected both cub production and first year survival. Annual cub and yearling recruitment rates were unrelated to maternal characteristics, except for a weak inverse relationship to HGB in lactating females ( $r^2 = 0.28$  and  $0.32$ , respectively,  $P < 0.03$ ,  $n = 17$ ).

In contrast, the annual biomass of yearlings raised by an individual female was associated with her condition, as it reflected not just the number of yearlings recruited but their weight at 14 months of age. Maternal LOGWT 2 months postpartum explained 69% ( $P \leq 0.0001$ ,  $n = 17$ ; Fig. 6) of the variation in yearling biomass and barren LOGWT explained 52% ( $P \leq 0.0001$ ,  $n = 16$ ). The only blood characteristic related to yearling biomass was HGB, which decreased with increasing biomass (Fig 6; lactating females:  $r^2 = 0.46$ ,  $P = 0.003$ ,  $n = 17$ ; nonlactating females:  $r^2 = 0.3$ ,  $P = 0.02$ ,  $n = 17$ ).

## DISCUSSION

### Litter Size

Our results suggest that some of the previously reported relationships between mother's weight and litter size may be spurious. Litter size in our study appeared to be related to maternal weight only because first-time mothers tended to be smaller and also produced smaller litters than multiparous females. In previous studies, first and subsequent litters were pooled for analysis, even though others also documented smaller litters for first-time mothers (Rogers 1987, Elowe and Dodge 1989, Beck 1991). Perhaps, then, some of the variation in litter size that has been attributed to differences in habitat and food supply (Rogers 1976, Beecham 1980, Reynolds and Beecham 1980, Eiler 1981, Alt 1989), or has been

correlated with maternal weight (Kolenosky 1990, Stringham 1990), was instead due to variation in reproductive maturity. Other studies, like ours, found no relationship between litter size and either maternal weight (Graber 1981, Beck 1991) or habitat quality (Schwartz and Franzmann 1991). Similarly, although there are conspicuous regional differences in litter size across the North American continent (Alt 1989, Beck 1991, Garshelis 1994), these trends do not appear to correspond with geographic differences in bear weights or habitat quality (Beck 1991, Garshelis 1994).

Conversely, although litter size may be unaffected by maternal weight within the weight range of most of the females in our study, litter size may change above or below a certain weight threshold. Pennsylvania females that produced litters of 4 and 5 cubs averaged 102 and 124 kg, respectively (Alt 1989), which matches the weight of the one exceptionally large female in our study (123 kg) that twice gave birth to 5 cubs. Mean weights of Pennsylvania females producing 1, 2, and 3 cubs were not significantly different ( $P > 0.05$ ), but this group was lighter than bears that produced 4 cubs, which in turn were lighter than those that produced 5 cubs (Alt 1989).

In our study, HGB in lactating females was related to litter size, but HGB in barren females was not. This suggests litter size affected HGB rather than HGB affecting litter size; females nursing litters of 3 or more cubs had lower HGB, as a consequence of greater lactational demands, than females with smaller litters. DelGiudice et al. (1991) suggested that depressed HGB values indicated an anemic response to nutritional stress in hibernating black bears. They observed the lowest values in lactating females during a winter following several years of very poor foods, and thus proposed that HGB could be an indicator of pre-hibernation dietary deficiency. Correspondingly, Hellgren et al. (1993) reported that HGB in active bears was higher in years of good food than in years of food shortage. Others also suggested a positive relationship between HGB and body condition (Schroeder 1987, Franzmann and Schwartz 1988, Hellgren et al. 1989), but season, sex, and age were possible confounding factors.

Although HGB values may reflect the population-wide nutritional plane, HGB may not be a good indicator of condition among individual females with cubs. In this study, females with the lowest HGB had the most cubs and also weaned the greatest yearling biomass, presumably indicating that they were in good condition and therefore supplied their young with large amounts of milk.

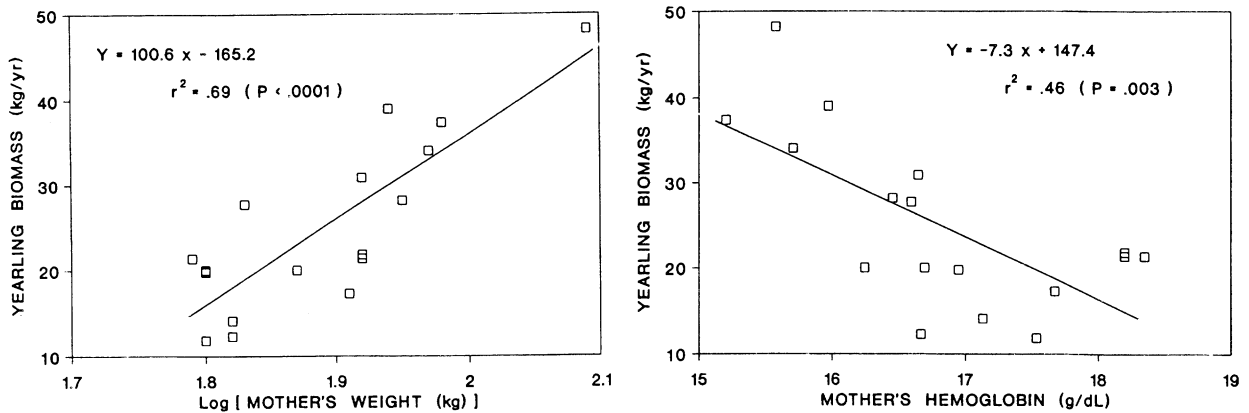


Fig. 6. Relationships between the log of maternal weight (2 months postpartum) and annual production of yearling biomass, and maternal hemoglobin and yearling biomass in black bears, north-central Minnesota, 1981-93. Values represent across-year means for individual females. (Annual yearling biomass for each female = total of all her yearling litter weights at 14 months of age/number of years over which they were produced).

### Sex of Cubs

We observed an increasing probability of producing male cubs with increasing maternal weight. To our knowledge, this is the first reported evidence for effects of maternal condition on sex ratios in bears. These results appear consistent with the model proposed by Trivers and Willard (1973). They suggested that females of polygynous species, whose condition and/or dominance rank influences the reproductive success of male offspring more than female offspring, should increase their output of males relative to females with improved maternal condition (better food). Considerable data supporting this theory from field studies of various species have been presented (Clutton-Brock et al. 1984, Clutton-Brock and Iason 1986, Thomas et al. 1989, Kojola and Eloranta 1989, and Kucera 1991). However, results of other studies suggest that when food is scarce, there is a selective advantage in producing more males than females, because males emigrate and are thus more apt to find better feeding areas, and are also less likely to compete with their mothers for food (Verme 1969, 1989; Clark 1978; Silk 1983; Cockburn 1985).

In black bears, large size may confer a disproportionately greater reproductive advantage for males than for females, since dominant males are assured access to multiple mates whereas nearly all mature females have similar breeding opportunities. Females attain sexual maturity at different ages, dependent on their birth weight, nurturing, and land inheritance from their mother, so there is also variance in female reproductive output corresponding with their mother's condition; nevertheless, this size-related variance in reproduction is likely less among females

than among males. Consequently, our results seem to support the Trivers and Willard (1973) theory, in that large females produced large, fast-growing, more male-biased cubs. Additionally, since single and twin cubs grew faster than triplets, males were more prevalent in small litters than in litters of 3. By extension, the lack of association between maternal condition and litter size may be partly attributed to the trade-off, faced by mothers in "average" condition, between producing a fast-growing litter of 1 or 2 males versus a slower growing litter of 3 cubs, with a higher percentage of females. It seems possible, then, that litter size could be influenced by external factors that favor a biased sex allocation among offspring, such as a harvest that skews the sex ratio of the population.

Most previous researchers concluded that sex ratios of black bear cubs did not differ from random expectation (Reynolds and Beecham 1980, Alt 1989, Elowe and Dodge 1989, Kolenosky 1990, Beck 1991), though most tallied somewhat more males than females. Perhaps cub sex ratios are often balanced by the conflicting effects of maternal condition and litter size. In Pennsylvania, for example, Alt (1982) originally reported that litters of 4 and 5 cubs had disproportionately more males than smaller litters. Later, however, presumably after observing male domination in both the largest and the smallest litters, he concluded that the pattern was not meaningful (Alt 1989). In fact, this pattern fits with what we observed in our study, as well as sexual allocation theory: there appears to be a threshold in maternal weight below which litter size is not affected (at least down to some lower level), but above which litter size increases with increasing maternal condition; accordingly, females in

superior condition should produce very large, male-dominated litters, whereas females in average condition might invest in either moderately-sized litters with a lower proportion of males, or small male-dominated litters.

We are unable to explain the relationships between sex ratio of cubs and blood characteristics. Typically, serum ALKP is high in juvenile bears but decreases with age (Brannon 1985b, Storm 1988 et al.) coincident with changes in osteoblastic activity associated with bone growth (Kaneko 1980). Our finding that high ALKP in adult bears corresponded with a higher percentage of male cubs and with larger cubs suggests a positive link with maternal condition. Seal and Hoskinson (1978) reported that in young pronghorns (*Antilocapra americana*) high ALKP was affiliated with good habitat quality, and Hawley (1987) noted that ALKP in bison (*Bison bison*) rose in response to high energy diets, although it decreased with high protein diets. However, Hellgren et al. (1993) found that relatively low ALKP, in both summer and winter black bear serum, coincided with years when food was plentiful, suggesting an inverse relationship with body condition. The specific origins of ALKP in hibernating adult bears have not been identified; liver, placenta, and bone are all potential sources (Kaneko 1980). Variations in ALKP among bears may reflect varying levels of metabolic activity in those tissues, and thus may not directly reflect body condition.

Associations between low CR in years between births and a more male-biased cub sex ratio, as well as higher weights in yearling offspring, suggests that CR may be linked to maternal condition. Creatinine results from the spontaneous breakdown of creatine, which occurs at a fairly constant rate. As CR is not altered by diet nor easily influenced by catabolism of protein, it is believed to reflect total body muscle mass (Kaneko 1980). In fasting animals, including bears, CR tends to increase (Brown et al. 1971, Nelson et al. 1973, Hellgren et al. 1990), probably as a result of decreased glomerular filtration (DelGiudice et al. 1987b). However, it does not continue to rise during hibernation (Hellgren et al. 1990, this study, unpubl. data), despite not being excreted in urine; this suggests that bears recycle CR during hibernation, as they do urea (Nelson et al. 1975). Variation in serum CR during hibernation may reflect not only muscle mass, but degree of body hydration (R. Nelson, Carle Foundation Hospital, Urbana, Ill., pers. commun.). Dehydration, which could elevate CR, may become more pronounced in bears with relatively low fat stores, as they would rely more heavily on muscle catabolism for energy, so less

metabolic water would be produced.

### Weight and Growth of Cubs

Our finding that litter weights were positively related to postpartum maternal weights was in accordance with a previous report (Rogers 1976) that fall weights of pregnant Minnesota black bears influenced the weight of their litters the following spring. The correspondence between mother's weight and the weights of individual cubs was not as clear, due to the additional influences of litter size and litter order. These confounding factors may explain why results of a Colorado black bear study indicated no relationship between cub weight and mother's weight (Beck 1991).

In this study, heavier cubs and heavier litters were associated with lower maternal MCV. This is consistent with previous studies, in which MCV in hibernating black bears was found to be lower following summers of abundant food than after food shortages (DelGiudice et al. 1991, Hellgren et al. 1993). Seal et al. (1978) demonstrated an inverse relationship between MCV in white-tailed deer (*Odocoileus virginianus*) and the quality of their habitat.

Interpretation of serum TP as an indicator of condition is unclear. Whereas low TP was associated with heavy cubs and litters, 2 young female bears in decidedly poor condition had low TP. The results of Hellgren et al. (1993) suggested an inverse relationship with condition, in that low TP during hibernation was typical of bears with previous access to supplemental food. However, in pronghorn antelope, elevated TP was linked to good habitat quality (Seal and Hoskinson 1978) and in moose (*Alces alces*), to good body condition (Franzmann and LeResche 1978). Changes in TP observed during fasting suggest that hemoconcentration and changes in body water balance may influence serum TP (DelGiudice et al. 1987a, 1987b). Thus, values for dormant bears probably should not be interpreted the same as for active animals.

### Cub Survival

Elowe and Dodge (1989) suggested that maternal condition affects the survival of offspring only when it drops below a certain threshold. We also suggest that such a threshold is likely; in our sample a maternal weight 2 months postpartum of at least 65 kg corresponded with 2-month-old cub weights >1.5 kg and 14-month-old offspring weights >10 kg, which appeared to be the weight limits that enabled survival of these age groups. Rogers (1976) reported a similar survival threshold for 2-month-old Minnesota cubs of

1.8 kg. Although cubs as small as 0.7 kg at 2 months old have survived (M. Obbard, Ontario Minist. Nat. Resour., Maple, Ont., pers. commun.), no one has examined a sufficiently large sample of lightweight cubs to reliably ascertain their survival rates. Although some studies indicated that cub survival may be affected by food supply (Rogers 1987, Eiler 1989), other studies found no such relationship (Alt 1989, Elowe and Dodge 1989, Schwartz and Franzmann 1991); the existence of a nutritional threshold might explain the disparity among studies.

### Age of First Reproduction

Our data indicate that juvenile bears in Minnesota must attain a March weight  $\geq 41$  kg before they are capable of producing cubs the following year. Beecham (1980) calculated that in 2 Idaho study areas, females had to weigh at least 50 kg by June-July in order to have cubs the next winter. Rogers (1976) previously suggested that both primiparous and multiparous female black bears had to reach at least 67 kg by fall in order to produce cubs that winter; he hypothesized that failure to gain adequate weight could lead to premature termination of pregnancy. This fall weight threshold has been cited widely (Kolenosky 1990, Beck 1991). However, reliance on fall weights may be misleading. Since pregnancy itself likely brings about physiologic changes that promote weight gain, it may not be appropriate to relate differences in reproductive success to differences between weights of pregnant and nonpregnant animals. Barren females that are lightweight in the fall and winter relative to pregnant females may be so in part because they are barren, rather than barren because they are lightweight. Examination of weights prior to and coincident with the breeding season may be more useful in ascertaining the influence of condition on reproductive success than fall weights, although it is also possible that a bear could be large enough to become pregnant, but not large enough in the fall to carry the pregnancy to term.

For juvenile bears  $\geq 41$  kg, body condition during late winter, as measured by WT/LN and CND, apparently forecasted condition later in the year, which influenced reproductive success. However, we are cautious about the use of WT/LN as an index of condition: weight is a function of volume, and volume increases with the cube of length, so WT/LN increases with length, even if body proportions do not change. This relationship likely explains why Schroeder (1987) found that most physiologic attributes that correlated with weight, age, and sex also correlated with WT/LN and WT/SK. Variations in WT/LN represent variations

in body proportion only for bears of similar length. In our study, pre-parous females  $\geq 41$  kg represented a subsample with a fairly narrow range in body lengths (123-158 cm), so WT/LN may have accurately reflected differences in condition. Our CND index was devised specifically to avoid the WT/LN ratio problem; this index compared a theoretical bear radius to length (WT was used in the equation only as a surrogate for volume), and thus should have declined with decreased fat, even with increased weight accompanying growth. However, age of first reproduction was the only reproductive parameter that was related more strongly to CND than to WT or LOGWT.

The direct relationship between hibernating juvenile CR and subsequent pregnancy is enigmatic. We posited earlier that CR is positively related to muscle mass and inversely related to fat. It may be that lean body mass carried into the breeding season is more critical for successful maturation and pregnancy than the previous winter's fat stores.

### Utility of Condition Indices in Bear Research and Management

Body weight in adult female black bears appears to be a good indicator of general nutritional condition and the potential to raise heavy litters of fast-growing offspring. For hibernating adult females, MCV, TP, and CR also seem to reflect condition; in conjunction with mother's weight, they improve regression models predicting size and growth rates of offspring. However, our results suggest that blood characteristics alone are not reliable indicators of condition. Similarly, Huot (1988) concluded, in his review of condition indicators in ungulates, that blood characteristics only augment assessments of condition based on body size.

Total lipids, CHL, RBC, and SUN do not correlate with reproductive parameters and appear to be unrelated to body condition in black bears. Only the negative correlation between SUN and body weight suggests a link to nutritional condition. In animals with access to food, high SUN generally indicates good nutrition (high protein intake; Warren et al. 1982), whereas in nutritionally deprived animals (such as hibernating bears), elevated SUN may indicate poor condition, reflecting an increased catabolism of body protein (Kirkpatrick et al. 1975, Warren et al. 1982, DelGiudice et al. 1987b).

The relationships between MCV, HGB, CR, TP, and reproductive parameters suggest areas for further investigation of physiologic function during hibernation. Particularly warranted are examinations

of how nutritional condition influences body water balance, metabolite recycling, and hematologic response to lactation. Without greater understanding of the processes controlling blood chemistry in animals that undergo long-term fasts, interpretation of blood values remains speculative.

For management purposes, a temptation exists to use nutritional indices as potential predictors of intrinsic growth and/or recruitment rates in black bear populations. Stringham (1990) reported correlations across populations between mean body weights and litter size, inter-litter interval, and age of first reproduction. However, his sample was limited to a small subset of hunted populations and he encountered numerous problems with lack of standardization among data from different studies. Garshelis (1994) found that mean yearling weights correlated with age of first reproduction across populations, and data from our study suggest that age of first reproduction is indeed the parameter most sensitive to nutritional condition. Litter size (Beck 1991) and cub survival (Beck 1991, Garshelis 1994), however, show wide variations across regions that are apparently unrelated to nutrition. Inferring differences in recruitment across regions from differences in condition indices thus seems unwise; although easier to collect, indices cannot replace direct determinations of litter size, cub survival, age of first reproduction and litter frequency. Furthermore, recent work by Coy and Garshelis (1992) and Carrel (1994) demonstrated that age of first reproduction and litter frequency can be determined from annular spacing in teeth, and any sampling scheme designed to obtain body measurements and/or blood samples would likely accommodate tooth collection as well.

Condition indices should be useful, though, as general indicators of underlying differences in habitat quality, and as such, can be helpful for investigating ecological relationships within or across populations. Spatial and temporal variation in habitat quality may influence movement patterns, land tenure, foraging strategies, and nuisance behavior, as well as reproduction. Direct assessments of habitat quality for bears based on vegetation is labor intensive and interpretations are obfuscated by uncertain differences in the quality of different food types (Noyce and Coy 1990); inferences of relative habitat quality based on adult female weight, yearling weight, and/or annual yearling biomass/adult female would be more easily obtained and should provide a sufficient basis for interpreting results of comparative studies.

## A Nutritional Model for Reproduction and Survival in Bears

In examining the sensitivities of different reproductive parameters to variations in body size and condition, we formulated a model for the nutritional regulation of reproduction and survival in black bears that is somewhat different from a previous model proposed by Eberhardt (1977) for long-lived species. He postulated that, as food resources become scarce, changes in life history parameters occur in the following sequence: (1) mortality rates of juveniles increase, (2) age of first reproduction increases, (3) reproductive rates of adult females decrease, and (4) adult mortality increases.

Our results suggest that for black bears, as the nutritional plane declines from a theoretical maximum, litter size is the first reproductive parameter to be affected (Fig. 7). Maximal litter sizes of 4 and 5 appear to be maintained only at near-maximal body weights. However, litter size does not show a continuous decline with diminished resources. Instead, bears seem to exhibit a modal litter size that is relatively unaffected across a broad range of maternal weights. We postulate that optimal litter size is influenced by mortality risks faced by cubs, and since cub survival is apparently unaffected by maternal condition over a broad range of maternal weights (above a weight threshold of 65 kg), optimal litter size may be related largely to mortality factors independent of food supply (e.g. predation [LeCount 1987], flooding of dens [Alt 1984], human-caused mortality [Beck 1991], inexperience of mothers [Elowe and Dodge 1989]). Accordingly, where mortality risks are high, relatively light mothers may produce more offspring that reach reproductive age by investing in litters of 3 relatively late-maturing young, rather than 1 or 2 faster-growing cubs. The modal young per litter thus may vary regionally, in response to mortality risks and maturation rates, but within a region it appears to be relatively constant.

Conversely, age of first reproduction is more variable both within a region (this study) and across regions (Garshelis 1994), as it is tied more closely with growth rates of cubs and hence the condition of the mother. Consequently, there appears to be a direct and persistent impact on reproductive age that spans the spectrum of varying resource availability (Fig. 7). However, there is likely an upper limit on the effect of maternal condition on maturation rates (even the most obese females will rarely produce young that

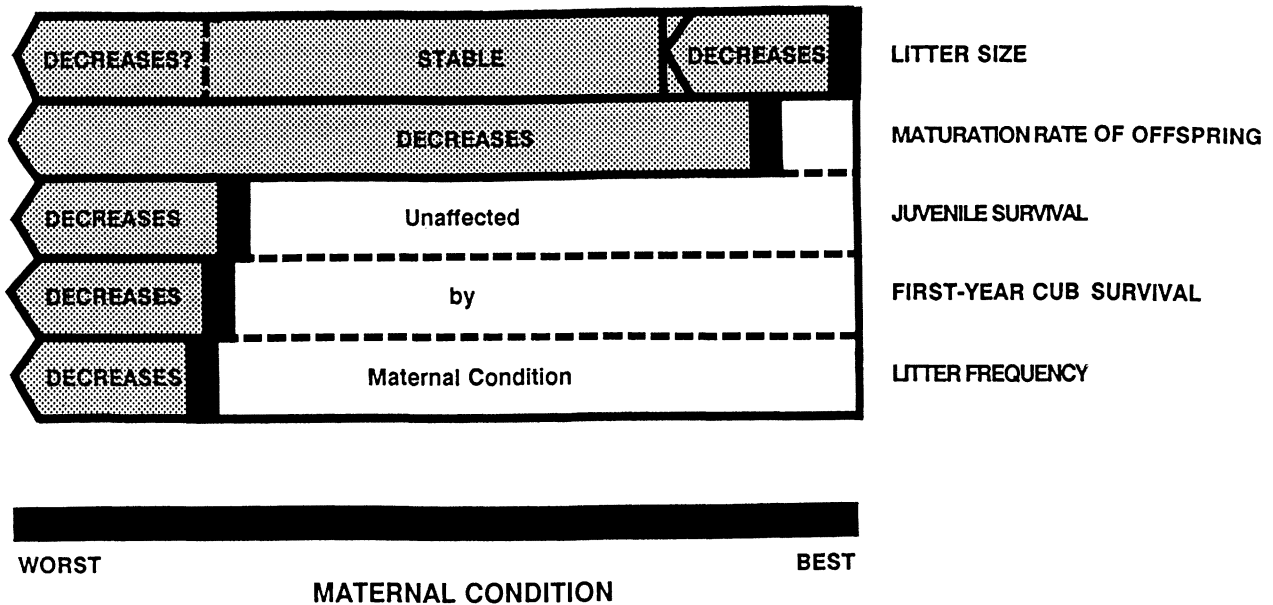


Fig. 7. Generalized model for the effects of maternal condition on life history parameters of black bears, based on data from north-central Minnesota, 1981-93, and published findings from other studies. Maximum rates of production, survival, and maturation of offspring are indicated by dark vertical bars at the right end of each arrow. Arrows denote decreasing values of reproductive parameters accompanying decreases in maternal condition, and by inference, decreases in nutrient availability.

mature before 2 years old); above this point increased reproductive success would be attained only with larger litters.

Juvenile survival rates appear to be affected only at very low levels of resource availability. This is in contrast to Eberhardt's (1977) suggestion that, for large mammals in general, juvenile survival is more sensitive than reproduction to diminished resources. In black bears, which have to deal with highly variable food supplies over a potentially long lifespan, it is probably adaptive to produce young that will survive all but the most severe food shortages and eventually reach reproductive age. In our study there was evidence that cub survival is more immune to declining resources than yearling survival. Only cubs <1.5 kg suffered increased first-year mortality, but cubs up to 2.2 kg ran a higher risk than heavier cubs of dying of starvation in their second year. At the point where resource levels get so low as to affect cub survival, one might expect to see a renewed response in litter size to maternal condition, since mothers could increase cub weights to the survival threshold by raising fewer per litter. However, our sample size of lightweight bears was not adequate to test this hypothesis.

Interval between litters also is affected only at markedly low resource availability. We saw no indication of extended reproductive intervals as a result

of depressed maternal condition (the cases we observed appeared unrelated to maternal condition), prompting us to speculate that food supplies must be at or below the level that causes an impact on cub survival to affect the reproductive interval of mature females. In other studies where food resources were notably poor, reproductive intervals that stretched to 3 or 4 years were more common (Jonkel and Cowan 1971, Rogers 1987, Miller 1994).

Finally, under Eberhardt's (1977) paradigm, extremely depauperate food conditions may reduce adult survival. No examples of adult natural mortality were witnessed in our study, and we are not aware of examples of adult starvation in the literature. However, since most adult black bear mortality is human-related, poor resources could affect adult survivorship by increasing attraction of bears to hunters' baits or to circumstances where they are disposed of as a nuisance. Thus, in present populations there may be little opportunity for adults to die naturally of poor condition.

Because of the heterogeneity of northern Minnesota forest habitat, females in our study spanned a fairly broad range of nutritional conditions, but only a few individuals approached either extreme. Thus, to some extent our conceptual model of the effects of resource availability, and consequently female condition, on life history parameters extends beyond the range of values

in our data. We have based some of our inferences upon results obtained from more extreme circumstances, such as the highly productive population studied by Alt (1989) in the eastern hardwood forests of Pennsylvania, and the apparently marginal populations studied by Miller (1994) and Kolenosky and Obbard (Ontario Minist. of Nat. Resour., Maple, Ont., pers. commun.). However, because of inconsistencies in the ways in which reproductive and survival parameter estimates are calculated and/or presented, a more thorough investigation of the relationships between these parameters and condition will likely require the collaborative efforts of researchers studying highly diverse populations.

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