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WEIGHTS AND HEMATOLOGY OF WILD BLACK BEARS DURING HIBERNATION

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ABSTRACT: We compared weights and hematological profiles of adult (>3-yr-old) female black bears (*Ursus americanus*) during hibernation (after 8 January). We handled 28 bears one to four times (total of 47) over 4 yr of varying mast and berry production. Mean weight of lactating bears was greater ($P < 0.0001$) than that of non-lactating females. White blood cells ($P < 0.05$) and mean corpuscular volume ($P = 0.005$) also differed between lactating and non-lactating bears. Hemoglobin ($P = 0.006$) and mean corpuscular hemoglobin concentration ($P = 0.02$) varied among years; values were lowest during 1975, following decreased precipitation and the occurrence of a second year of mast and berry crop shortages in a three-year period. Significant ($P < 0.05$) interaction between reproductive status (lactating versus non-lactating) and study year for hemoglobin, red blood cells, and packed cell volume, and increased mean corpuscular volume, suggested a greater nutritional challenge for lactating females compared to non-lactating females during the 1975 denning season. Our data suggest that hematological characteristics of denning bears may be more sensitive than weights as indicators of annual changes in nutritional status; however, other influential factors, in addition to mast and berry crop production, remain to be examined.

Key words: Black bear, body weight, hematology, hibernation, lactation, nutritional assessment, *Ursus americanus*.

INTRODUCTION

Hematologic profiles of bears (*Ursus* spp.) have been used to examine seasonal patterns of metabolism, nutritional condition, and the influence of age, sex, and location (Seal et al., 1967; Pearson and Halloran, 1972; Matula et al., 1980; Nelson et al., 1983; Brannon, 1985; Schroeder, 1987; Franzmann and Schwartz, 1988; Hellgren et al., 1989). Specifically, hemoglobin (Hb) and packed cell volume (PCV) may be used as sensitive indicators of seasonal changes in body condition of black bears (*U. americanus*) (Schroeder, 1987; Franzmann and Schwartz, 1988; Hellgren et al., 1989). However, there is little information concerning the hematology of black bears during hibernation, particularly relative to condition. Black bears in northeastern Minnesota hibernate for 5 to 7 mo from late September to April (Rogers, 1987). While denning, bears do not eat, drink, urinate, or defecate, and relying primarily on fat catabolism, they burn approximately 4,000 kcal/day (Nelson, 1973, 1980). Furthermore, cubs are born to gravid females during the latter part of the denning period. Thus, these females incur the added energetic cost of lactation (Jonkel, 1978).

Between 1971 and 1976, Minnesota bears endured four years (1972, 1974–76) of dramatic shortages of mast (primarily *Corylus cornuta*) and berries (mainly *Vaccinium* spp., *Prunus* spp., *Cornus* spp., and *Rubus* spp.), which are important dietary components for black bears in the study area (Rogers, 1976a, b). Poor mast and berry crops have been associated with undernutrition in black bears. Specifically, bears have shown insufficient weight gain prior to denning, emaciation, and reduced reproductive success reflected by depressed growth, development, and survival of cubs and yearlings (Hatler, 1967; Jonkel and Cowan, 1971; Rogers, 1976a, 1987). Our objective for the present study was to document weights and hematological profiles of lactating and non-lactating, adult, female black bears during hibernation and to determine if crop failures prior to denning were reflected by changes in weights and hematology.

STUDY AREA

This study was concentrated in a 300-km² area of the Superior National Forest of northeastern Minnesota (Rogers, 1987). Vegetation was 76% upland and 24% lowland; approximately 59% of the upland was mixed coniferous-deciduous communities (Peek et al., 1976). Aspens (*Populus* spp.), paper birch (*Betula papyrifera*), red pine (*Pinus resinosa*), jack pine (*P. banksiana*), white pine (*P. strobus*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*) were common on uplands. Black spruce (*Picea mariana*), balsam fir, white cedar (*Thuja occidentalis*), black ash (*Fraxinus nigra*), and paper birch were predominant on lowlands (Maycock and Curtis, 1960). The climate is cool-temperate. During the study, average annual snowfall was 157 cm. Snow cover is nearly continuous from mid-November to mid-April (Rogers, 1987). From April to September (bears' active period), mean daily minimum ambient temperatures ranged from −5 to 14.2 C; mean daily maximum temperatures ranged form 8.3 to 27.9 C (National Oceanic and Atmospheric Administration, 1971, 1972, 1973, 1974). Total precipitation during these months was 50, 63, 64, and 40 cm for 1971, 1972, 1973, and 1974, respectively (National Oceanic and Atmospheric Administration, 1971, 1972, 1973, 1974).

MATERIALS AND METHODS

Radio-collared adult (≥3-yr-old) female bears were tracked to their dens between 8 January and 18 April 1972 to 1975 and were injected intramuscularly by pole syringe with 0.2 mg/kg of phencyclidine hydrochloride and 0.5 mg/kg of promazine hydrochloride. Induction of anesthesia occurred within 2 to 10 min. Immobilized bears were eartagged, weighed with a spring scale to the nearest 0.45 kg, and physically examined. A first upper premolar was extracted for age estimation by analysis of cementum annuli (Willey, 1974). Ten to 30 min after induction, blood was collected from a femoral vein by venipuncture into a 5-ml ethylenediamine tetraacetate vial. Blood samples were kept cool and analyzed within 72 hr. Hematologic analyses were conducted as described by Seal et al. (1967).

Mean ages and weights of bears were compared by two-way analysis of variance and covariance, respectively. Year (1972 to 1975) and reproductive status (lactating, non-lactating) were the factors in both analyses; age (years) was the covariate. We similarly analyzed hematologic data by two-way analysis of covariance using weight as the covariate. Only non-pregnant, non-lactating females were compared to lactating bears, and only data collected during a single handling of each bear per hibernation period were included in analyses. Multiple group comparisons were made by Tukey's studentized multiple-range test at $P \leq 0.05$. Data are presented as mean ± standard errors (SE). The minimum acceptable level of significance was $P \leq 0.05$.

RESULTS

Twenty-eight hibernating bears were chemically immobilized and handled one to four times during the 4 yr study; 47 blood samples were collected. Approximately 79% of the samples were collected during March. There was no difference in age between lactating (8.9 ± 0.6 yr, range = 5 to 14 yr, $n = 19$) and non-lactating (7.7 ± 0.7 yr, range = 3 to 14 yr, $n = 28$) bears. Mean weight of lactating bears (range = 56.4 to 85.0 kg) was 24% greater ($P < 0.0001$) than that of non-lactating bears (range = 30.5 to 68.2 kg) (Table 1). Mean age (8.2 ± 0.5 yr, $n = 47$) and weight (58.8 ± 1.8 kg, $n = 47$) did not differ among years (Table 2). Of the variables examined, reproductive status (lactating versus non-lactating) was most strongly related to the variability of weight [Weight (kg) = $84.7 - 16.3x$, x = reproductive status, $R^2 = 0.40$]. Age was a significant ($P < 0.01$) covariate; however, the relationship to weight was not clear. Of bears weighed during March, lactating bears were 27% heavier ($P < 0.001$) than non-lactating bears (68.8 ± 1.9 kg versus 50.1 ± 2.7 kg, n = 18 and 19, respectively).

Mean white blood cell (WBC) counts and mean corpuscular volume (MCV) differed ($P < 0.05$ and $P < 0.005$) between lactating (range = 4.5 to 11.0 $10^3/\mu l$ and 59 to 75 fl, respectively) and non-lactating (range = 3.9 to 18.8 $10^3/\mu l$ and 51 to 72 fl, respectively) bears (Table 1). The

TABLE 1. Significant effects of lactation on weight and hematological characteristics of adult (≥3-yr-old) female black bears, Superior National Forest, northeastern Minnesota, 8 January to 18 April 1972 to 1975.

Characteristics	Lactating			Non-lactating		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Weight (kg)	68.4[a]	1.6	19	52.2	2.0	28
White blood cells ($10^3/\mu l$)	6.7[b]	0.3	19	7.5	0.6	28
Mean corpuscular volume (fl)	66.4[c]	1.2	19	63.1	0.7	28

[a] Lactating differed ($P < 0.0001$) from non-lactating.
[b] Lactating differed ($P < 0.05$) from non-lactating.
[c] Lactating differed ($P < 0.005$) from non-lactating.

greatest difference in MCV occurred in 1975. Mean Hb ($P = 0.006$) and mean corpuscular hemoglobin concentration (MCHC, $P = 0.02$) varied from 1972 to 1975. Mean PCV tended ($P = 0.06$) to differ among years. Hemoglobin and MCHC were lowest during 1975. Hemoglobin was lower ($P < 0.05$) during 1975 (16.9 ± 0.4 g/dl , range = 14.1 to 19.5 g/dl, $n = 12$) than in 1974 (18.7 ± 0.3 g/dl, range = 16.5 to 20.8 g/dl, $n = 14$). Mean corpuscular hemoglobin concentration was lower ($P < 0.05$) in 1975 (33.5 ± 0.3 g/dl, range = 31 to 35 g/dl, $n = 12$) compared to 1973 (35.5 ± 0.5 g/dl, range = 33 to 38 g/dl, $n = 10$).

There was a significant interaction between reproductive status and year for Hb ($P = 0.04$), red blood cell (RBC) counts ($P = 0.004$), and PCV ($P = 0.02$) (Table 2). Mean Hb, RBC, and PCV of lactating bears were stable until 1975 when values decreased. In contrast, Hb, RBC's, and PCV of non-lactating females were diminished during 1972, increased through 1974, then decreased by 1975.

DISCUSSION

The greater weights of lactating bears compared to non-lactating bears during hibernation were consistent with the weight disparity observed just prior to denning of adult females that produced cubs (>80 kg) versus those that did not (<67 kg) (Rogers, 1976b). The mean weight of our lactating bears during all 4 yr was <80 kg due to weight loss during hibernation. Weight losses of wild bears during hibernation range from 16 to 37% (Tietje and Ruff, 1980; Hellgren et al., 1990).

Absence of significant variation in weights among years demonstrated that shortages of mast and berry crops were not severe enough to diminish body mass of adult females. However, these food shortages resulted in underweight cubs, yearlings, and subadults and starvation losses in these age classes (Rogers, 1987). Hellgren et al. (1989) observed significant ($P = 0.03$) seasonal variation in weights of female black bears associated with dietary changes, but the variation was primarily attributable to subadults. Thus, it is apparent that young bears are less capable of maintaining their weight during periods of diminished availability of nutritious foods.

With only a 11% difference in mean WBC counts of lactating and non-lactating bears, values in both were similar to those reported by Hellgren et al. (1989) for wild, female black bears (three lactating, one non-lactating) during hibernation (7.1 ± 1.0 × $10^3/\mu l$); however, counts were considerably higher during non-denning seasons in that study. Matula et al. (1980) also observed higher WBC concentrations (10.2 ± 0.5 × $10^3/\mu l$, $n = 44$) in non-denning black bears. The larger MCV of lactating bears suggests that they may have been recovering from an anemia associated with pregnancy (Benjamin, 1981, p. 133). Hematological values may decline 20 to 35% in dogs (*Canis familiaris*) during pregnancy (Anderson and Gee, 1958; Tietz et al., 1967; Concannon et al., 1977).

TABLE 2. Age and hematological characteristics of lactating and non-lactating, adult (≥3-yr-old) female black bears during hibernation, Superior National Forest, northeastern Minnesota, 8 January to 18 April 1972 to 1975.

Character-	1972						1973						1974						1975					
	Lactating			Non-lactating			Lactating			Non-lactating			Lactating			Non-lactating			Lactating			Non-lactating		
istics[a]	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Age (yrs)	7.0	1.1	5	8.0	1.4	6	11.7	0.3	3	5.9	1.3	7	8.1	1.0	7	7.0	1.7	7	10.5	2.4	4	9.6	1.6	8
Weight (kg)	65.1	3.5	5	57.3	4.8	6	68.0	4.6	3	50.0	5.7	7	71.2	3.1	7	53.8	3.8	7	68.1	3.1	4	48.9	2.8	8
Hb (g/dl)[b]	18.3	1.0	5	15.7	0.9	6	19.1	1.1	3	18.7	0.8	7	18.2	0.4	7	19.3	0.4	7	15.9	0.6	4	17.4	0.5	8
RBC (10^6/ul)[c]	8.3	0.4	5	7.4	0.5	6	8.4	0.4	3	8.2	0.3	7	8.2	0.3	7	8.8	0.2	7	6.6	0.4	4	8.5	0.3	8
PCV (%)[b]	54.2	2.7	5	45.5	3.0	6	53.0	2.0	3	52.3	2.3	7	53.4	1.3	7	55.6	1.1	7	46.5	1.7	4	52.4	1.8	8
WBC (10^3/ul)	6.4	0.7	5	8.7	1.9	6	6.2	0.2	3	6.0	0.7	7	6.4	0.5	7	6.5	0.7	7	8.0	1.1	4	8.8	1.6	8
MCV (fl)	65.6	1.8	5	62.7	2.4	6	63.0	1.5	3	64.0	0.9	7	66.0	3.0	7	63.6	1.5	7	70.5	1.8	4	62.1	1.3	8
MCHC (g/dl)	33.6	0.5	5	34.7	0.5	6	35.7	0.9	3	35.4	0.7	7	35.0	0.8	7	34.6	0.5	7	34.3	0.3	4	33.1	0.5	8

[a] Hb = hemoglobin, RBC = red blood cells, PCV = packed cell volume, WBC = white blood cells, MCV = mean corpuscular volume, and MCHC = mean corpuscular hemoglobin concentration.

[b] Significant ($P < 0.05$) interaction between year and lactating status.

[c] Significant ($P = 0.004$) interaction between year and lactating status.

Lowest Hb and MCHC values during 1975, indicated a hypochromic anemia (Benjamin, 1981, p. 133). Matula et al. (1980) suggested that a microcytic hypochromic anemia in young, growing black bears during non-denning seasons was related to greater iron requirements compared to adults. The anemia evident in our bears may have been a more sensitive indicator than weight of either cumulative dietary deficiencies, specifically of iron and/or copper (Benjamin, 1981, p. 133), by the end of the second year (1974) of poor crop availability or simply, of more severe deficiencies during 1974. Total precipitation during the bears' active period (April to September) in 1974 was 20% less than in 1971, and 38% less than in 1972 and 1973 (National Oceanic and Atmospheric Administration, 1971, 1972, 1973, 1974). The interaction between reproductive status and year for Hb, RBC count, and PCV, and increased MCV values in lactating females, indicated that during 1975 the nutritional challenge was greater for these bears than for non-lactating females.

In contrast, the influence of factors other than mast and berry production on nutritional status and hematology is suggested by the low Hb concentrations, RBC counts, and PCV's of denning, non-lactating bears during 1972. These diminished values occurred in bears after several years of mast and berry crop abundance (Rogers, 1976a, b).

Recently, studies have demonstrated that during non-denning seasons Hb, RBC, and PCV are sensitive indicators of the nutritional condition of black bears (Schroeder, 1987; Franzmann and Schwartz, 1988; Hellgren et al., 1989). Mean Hb (21.1 ± 1.0 g/dl), RBC (10.3 ± 1.3 × $10^6/\mu l$), and PCV (61 ± 2.2%) of captive, denning black bears in Michigan, previously maintained on commercial dog food, were greater than for our wild bears (Erickson and Youatt, 1961), and suggests poorer condition of the latter. Seasonal changes in these hematological characteristics and significant ($P <$

0.01) correlations with physical condition indices have been observed in free-ranging bears (Hellgren et al., 1989). Denning females ($n = 4$) in that study, exhibited mean Hb (16.9 $\pm$ 0.5 g/dl) and PCV (48.0 $\pm$ 1.4%) comparable to the lower values of our bears (1972 and 1975). Franzmann and Schwartz (1988) reported lower Hb concentrations for females in poor condition (17.0 $\pm$ 2.0 [SD] g/dl) compared to those in good condition (22.2 $\pm$ 4.1 g/dl) during the non-denning portions of the year. Denning females ($n = 9$) had mean Hb (18.9 $\pm$ 1.4 g/dl) and PCV (51.9 $\pm$ 5.8%) values similar to the higher values of our bears (Franzmann and Schwartz, 1988).

Because black bear physiology changes dramatically during hibernation, it seems inappropriate to use hematological values to assess and compare the condition of denning black bears to non-denning bears during the remainder of the year (Folk, 1966, pp. 194–201; Franzmann and Schwartz, 1988). However, our data suggest that hematological analysis may be useful as a sensitive means of evaluating annual changes in the condition of denning bears and for examining effects of lactation. We have provided reference values for weights and hematological characteristics of wild, adult female bears during hibernation, following years of good and poor availability of natural food supply. Assessment of nutritional condition based on hematological indices may provide methods of comparison between the physiological status of black bear populations and habitat quality. However, supplemental feeding at garbage dumps by bears and availability of seasonal food items other than mast and berries may affect their nutritional status (Rogers, 1987); therefore these factors should also be examined relative to their hematology. Results of such investigations can clarify forest management options that maintain or enhance diversity and abundance of mast producing species and productivity of bear populations within regions susceptible to failures in forage production (Rogers et al., 1988). Younger bears have been more vulnerable to starvation during years of food shortage (Rogers, 1987). Future research should focus on the relationship of food supply to weights and hematological profiles of denning cubs, yearlings, and subadults.

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LITERATURE CITED

ANDERSON, A. C., AND W. GEE. 1958. Normal blood values in the beagle. Veterinary Medicine 53: 135–139.

BRANNON, R. D. 1985. Hematological characteristics of grizzly bears (*Ursus arctos*) in central and northeastern Alaska. Canadian Journal of Zoology 63: 58–62.

BENJAMIN, M. M. 1981. Outline of veterinary pathology. The Iowa State University Press, Ames, Iowa, 351 pp.

CONCANNON, P. W., M. E. POWERS, W. HOLDER, AND W. HANSEL. 1977. Pregnancy and parturition in the bitch. Biology of Reproduction 16: 517–526.

ERICKSON, A. W., AND W. G. YOUATT. 1961. Seasonal variations in the hematology and physiology of black bears. Journal of Mammalogy 42: 198–203.

FOLK, G. E., JR. 1966. Introduction to environmental physiology. Lea and Febiger, Philadelphia, Pennsylvania, 308 pp.

FRANZMANN, A. W., AND C. C. SCHWARTZ. 1988. Evaluating condition of Alaskan black bears with blood profiles. The Journal of Wildlife Management 52: 63–70.

HATLER, D. F. 1967. Some aspects in the ecology of the black bear (*Ursus americanus*) in interior Alaska. M.S. Thesis. University of Alaska, College, Alaska, 111 pp.

HELLGREN, E. C., M. R. VAUGHAN, AND R. L. KIRKPATRICK. 1989. Seasonal patterns in physiology and nutrition of black bears in Great Dismal Swamp, Virginia–North Carolina. Canadian Journal of Zoology 67: 1837–1850.

———, ———, ———, AND P. F. SCANLON. 1990. Serial changes in metabolic correlates of hibernation in female black bears. Journal of Mammalogy 71: 291–300.

JONKEL, C. J. 1978. Black, brown (grizzly), and polar bears. *In* Big game of North America, ecology and management, J. L. Schmidt and D. L. Gilbert (eds.). Stackpole Books, Harrisburg, Pennsylvania, pp. 227–248.

———, AND I. MCT. COWAN. 1971. The black bear in the spruce-fir forest. Wildlife Monograph 27, The Wildlife Society, Washington D.C., 57 pp.

MATULA, G. J., JR., J. S. LINDZEY, AND H. ROTHENBACHER. 1980. Sex, age, and seasonal differences in the blood profile of black bears captured in northeastern Pennsylvania. International Conference on Bear Research and Management 4: 49–56.

MAYCOCK, A. C., AND J. T. CURTIS. 1960. The phytosociology of boreal conifer-hardwood forests of the Great Lakes Region. Ecological Monograph 30: 1–35.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION. 1971. Climatological data: Minnesota. National Climatic Center, Asheville, North Carolina.

———. 1972. Climatological data: Minnesota. National Climatic Center, Asheville, North Carolina.

———. 1973. Climatological data: Minnesota. National Climatic Center, Asheville, North Carolina.

———. 1974. Climatological data: Minnesota. National Climatic Center, Asheville, North Carolina.

NELSON, R. A. 1973. Winter sleep in the black bear: A physiologic and metabolic marvel. Mayo Clinic Proceedings 48: 733-737.

———. 1980. Protein and fat metabolism in hibernating bears. Federation Proceedings 39: 2955-2958.

———, D. L. STEIGER, AND T. D. I. BECK. 1983. Neuroendocrine and metabolic interactions in the hibernating black bear. Acta Zoologica Fennica 174: 137–141.

PEARSON, A. M., AND D. W. HALLORAN. 1972. Hematology of the brown bear (*Ursus arctos*) from southwestern Yukon Territory, Canada. Canadian Journal of Zoology 50: 279–286.

PEEK, J. M., D. L. URICH, AND R. J. MACKIE. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monograph 48, The Wildlife Society, Washington D. C., 65 pp.

ROGERS, L. L. 1976a. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Ph.D. Thesis. University of Minnesota, Minneapolis, Minnesota, 194 pp.

———. 1976b. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions of the North American Wildlife and Natural Resources Conference 41: 431–438.

———. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildlife Monograph 97, The Wildlife Society, Washington D. C., 72 pp.

———, G. A. WILKER, AND A. W. ALLEN. 1988. Managing northern forests for black bears. *In* Integrating forest management for wildlife and fish. U.S. Department of Agriculture General Technical Report NC-122, North Central Forest Experiment Station, St. Paul, Minnesota, pp. 36–42.

SCHROEDER, M. T. 1987. Blood chemistry, hematology, and condition evaluation of black bears in northcoastal California. International Conference on Bear Research and Management 7: 333-349.

SEAL, U. S., W. R. SWAIM, AND A. W. ERICKSON. 1967. Hematology of the Ursidae. Comparative Biochemical Physiology 22: 451–460.

TIETJE, W. D., AND R. L. RUFF. 1980. Denning behavior of black bears in the boreal forest of Alberta. The Journal of Wildlife Management 44: 858–870.

TIETZ, W. J., M. M. BENJAMIN, AND G. M. ANGLETON. 1967. Anemia and cholesterolemia during estrus and pregnancy in the beagle. American Journal of Physiology 212: 693–697.

WILLEY, C. H. 1974. Aging black bears from first premolar tooth sections. The Journal of Wildlife Management 38: 97–100.

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