

SPRING WEIGHT CHANGES IN BLACK BEARS IN NORTHCENTRAL MINNESOTA: THE NEGATIVE FORAGING PERIOD REVISITED

KAREN V. NOYCE, Minnesota Department of Natural Resources, 1201 East Highway 2, Grand Rapids, MN 55744, USA, email: karen.noyce@dnr.state.mn.us

DAVID L. GARSHELIS, Minnesota Department of Natural Resources, 1201 East Highway 2, Grand Rapids, MN 55744, USA, email: dave.garshelis@dnr.state.mn.us

Abstract: The term “negative foraging period” has been used to describe the time between the emergence of black bears (*Ursus americanus*) from their dens and the ripening of fleshy fruits in summer; the implication is that spring foods lack adequate energy for bears to gain or even maintain weight. Few biologists, however, have examined data on weight changes to determine if the concept applied to the bears they studied. We investigated age and sex-specific weight changes of black bears in northcentral Minnesota between denning and early July. Weights were obtained from bears trapped ($n = 350$) or handled at dens ($n = 270$) during 1981–89. Weights of 1- to 2-year-old males and females rose from late winter (Feb–Mar) to late spring (May–early Jun) and again from late spring to early summer (early Jun–mid-Jul), with gains averaging 8–14 kg over the period. Bones (head length) of young bears also grew during spring, although chest girth decreased, indicating loss of fat. Mean weights of 4- and 5-year-old males increased 21 and 10 kg, respectively, from winter to late spring, but decreased 20 and 25 kg between late spring and early summer. Only males ≥ 6 years old lost weight during both periods ($\bar{x} = 16$ kg). Behavioral and physiological changes associated with breeding, including increased testosterone, increased activity, and decreased feeding, probably explained most weight loss in breeding-age males. In females, most weight loss was associated with lactation. Lactating females either lost weight from winter to early summer (sequential weights of individuals) or showed no significant change (mean weights of pooled sample), whereas non-lactating adult females gained weight. Despite a spring diet that is generally low in carbohydrates and fats, bears apparently make efficient use of plant protein. Past studies, with small samples and data pooled among sex–age groups, did not recognize the importance of spring as a period of growth for young bears.

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Key words: black bears, growth, “negative foraging period”, nutrition, spring foods, weight changes, *Ursus americanus*.

After emerging from dens in the spring, and until fruits ripen in summer, black bears in most parts of North America subsist on a diet comprised largely of green vegetation, supplemented in some places with colonial insects, primarily ants (Hymenoptera) (McDonald and Fuller 1993). Spring foods have been considered only marginally nutritious for bears (Jonkel and Cowan 1971, Rogers 1976, Beeman and Pelton 1980, Eagle and Pelton 1983), who lack a rumen or cecum to help digest cellulose.

Jonkel (1960) introduced the term “negative foraging period” to describe a time following den emergence when black bears in Montana lost weight, implying that available spring foods provided insufficient energy for them to maintain body mass. The phrase was used again by Poelker and Hartwell (1973), who suggested that the dietary shift by Washington black bears from sapwood to salmonberry (*Rubus spectabilis*) marked transition from the negative to the positive foraging period, though they presented no data on weight changes of bears during that time. Since then, other researchers have attributed spring weight losses in bears to the negative foraging period (Beeman 1975, Beecham 1980, Hellgren et al. 1989), despite small sample sizes and inconclusive trends, or have invoked the concept in interpreting local bear demographics, despite lack of data on weight change in their study populations (Landers et al. 1979, Clark et al. 1987, MacHutchon 1989). Moreover, in some studies, black

bears have not lost weight during spring (Pelchat 1979, Graber 1981). Thus, the applicability of the concept of a negative foraging period remains unclear.

We obtained weights and other body measurements for black bears in Minnesota over 9 years and investigated patterns of spring weight change and growth by sex, age, and reproductive status. Our null hypothesis was that bears would not gain weight or grow skeletally on a spring diet.

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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 northcentral Minnesota, approximately 30 km north of Grand Rapids. The area was >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*) dominated on the uplands with lesser amounts of conifer (*Pinus resinosa*, *P. strobus*, *Picea glauca*) and hardwoods (*Acer saccharum*, *Tilia americana*, *Quercus rubra*, *Q. macrocarpa*). Lowland forests of black spruce (*Picea mariana*), tamarack (*Larix laricina*), northern white cedar (*Thuja occidentalis*), and black ash (*Fraxinus nigra*) comprised approximately 33% of the forested area.

In this area, most bears exited their dens in early or mid-April (Garshelis 1987). From April–June, green vegetation, including wild calla (*Calla palustris*), clover (*Trifolium* spp.), graminoids, dandelions (*Taraxacum officinale*), and newly emergent leaves and catkins of quaking aspen were the herbaceous foods most commonly eaten by bears; ants were a major component of the diet in June and early July (Garshelis et al. 1988). A variety of berries was available for summer forage; some ripened in early July, but none were plentiful until about mid-July (K.V. Noyce, Minnesota bear food survey: 10-year summary, 1982–91, St. Paul, 1992). In the fall, hazel (*Corylus* spp.) and oak provided bears with nuts, but mast quantity was highly variable across time and space (Noyce and Coy 1990; K.V. Noyce 1992 unpubl. rep.; Noyce and Garshelis 1997).

METHODS

Bears were captured, mainly in baited barrel traps, and most were fitted with radiocollars (171 males, 103 females) during May–July 1981–89; radiocollared bears also were handled annually in their dens during December or February–March, 1981–89. We immobilized bears with either a mixture of ketamine hydrochloride (11–13 mg/kg) and promazine (0.6–0.7 mg/kg) or premixed tiletamine hydrochloride and zolazepam (Telazol®, Elkins-Sinn, Inc., Cherry Hill, N.J., 3.9–5.3 mg/kg). We extracted a first upper premolar for age estimation from cementum annuli (Willey 1974). Bears were weighed to the nearest pound using hanging spring scales, and weights were converted to kilograms. We recorded body measurements to the nearest cm, including head length (tip of nose to intersection of sagittal and lambdoidal crests) and chest girth after exhale. We used increased head length to indicate skeletal growth because this measurement varied little among different observers and was virtually unaffected by thickness of subcutaneous fat. We assumed that chest girth reflected both size of the body frame and thickness of back fat and interpreted decreases in chest girth in individual bears as depletion of back fat.

We discounted weights obtained after the third capture of any bear in a single year to reduce the possible effects of our baits (0.4–1.0 kg bacon available at each trap site) on weight gain. We also omitted weights of bears known to visit either of 2 garbage dumps in our study area during the spring, based on capture and telemetry locations obtained at least weekly. At 1 dump site, we monitored frequency and duration of visits by radiocollared bears (up to 15 individuals concurrently) using an event recorder and scanning receiver (Garshelis 1987) during 1984–89. We monitored the other dump site during 1987–89. In 1987, both dumps were converted to solid waste transfer stations with locked dumpsters, and food was no longer available to bears.

We categorized weights into 3 seasons: late winter (3 Feb–31 Mar, median handling date 11 Mar), late spring (11 May–7 Jun, median 2 Jun), and early summer (8 Jun–15 Jul, median 24 Jun). The split between late spring and early summer roughly coincided with the shift from herbaceous to herbaceous–insectivorous feeding (Garshelis et al. 1988) and with the start of the breeding season (Garshelis and Hellgren 1994). The end of the early summer roughly matched the time when berries became available (K.V. Noyce, 1992, unpubl. rep.).

We used 620 weights from 257 bears; 128 bears were weighed only once in the 9-year study and 129 were weighed ≥ 2 times. For bears weighed more than once during the late spring of 1 year, we used the earliest weight, as it was most indicative of changes shortly after den emergence and least likely to be influenced by consumption of trap baits. For bears trapped more than once during the early summer, we used the last weight, as this was most indicative of changes since late spring. However, if a bear was captured >3 times, we used the last weight obtained in the first 3 captures. We categorized bears 1–5 years old in 5 age groups, so no bears <6 years old were included more than once in a seasonal, age-specific data set. However, bears ≥ 6 years old were grouped together, so those that were weighed during the same season in different years ($n = 29$) contributed >1 weight to the sample. Because these data included some repeated measures of the same individual, some P values may have been underestimated.

We log-transformed weights (LOGWT) to more closely approach a normal distribution and calculated means by season, sex, age (1, 2, 3, 4, 5, ≥ 6 years), and, for females, reproductive status (lactating or non-lactating). We compared means of LOGWTs using 2 runs of a 3-way analysis of variance for unbalanced sample sizes. We tested for all main effects plus 2-way and 3-way interactions with the GLM Procedure (SAS Inst., Inc. 1990) and used

the contrast option to test differences between seasons for individual sex–age groups. In the first run, we included only adult age classes (4, 5, and ≥ 6 years old) and categorized bears into 3 sex–reproductive classes (male, non-lactating female, and lactating female), in order to examine the effects of reproductive status, season, and age on weight. The second run included bears of all ages, but excluded lactating females (whose inclusion would have introduced too many empty cells into the analysis as no yearlings, no 2-year-olds, and very few 3-year-olds lactated) and tested for the effects of sex, season, and age. To guard against Type II errors resulting from small samples and high within-cell variance, we chose $\alpha = 0.1$ for all analyses.

In a second analysis, we used only individuals weighed more than once in 1 year and compared sequential weights using Wilcoxon's signed-rank test. We calculated net rates of average daily weight gain or loss for each bear (kg/day) and compared median weight change by sex–age group and season. To estimate gains or losses most representative of the first 2 months after emergence from dens, when bears were not breeding and ate mostly vegetation, we compared weights of individuals handled in late winter and again in late spring or individuals handled twice ≥ 6 days apart during late spring. For changes representative of the late spring to early summer transition, when bears were breeding and ate large quantities of ants, we used pairs of weights from bears handled in late spring and early summer or twice, ≥ 6 days apart, during early summer.

RESULTS

Mean Weights by Age, Sex, and Season

Males and non-lactating females exhibited seasonal changes in LOGWT between late winter and early summer ($F = 126.3$, 534 df, $P \leq 0.0001$), but seasonal effects varied among age classes (age \times season interaction: $F = 5.85$, 10 df, $P \leq 0.0001$) and age differences varied by sex (age \times sex interaction: $F = 15.6$, 5 df, $P \leq 0.0001$). Weights of 1- and 2-year-old males increased significantly from late winter to early summer ($P \leq 0.0001$ and $P = 0.002$, respectively). Weight gain averaged 10.5 and 14.1 kg for 1- and 2-year-old males, respectively, representing increases of 48% and 35% over late winter weights (Table 1). Weights of 4-year-old males increased between late winter and late spring ($P = 0.02$) but then dropped, as did weights

of 5-year-olds, from late spring to early summer ($P = 0.03$ and $P = 0.1$, respectively). Males ≥ 6 years old lost weight from late winter to early summer ($P = 0.08$).

Like males of the same age, mean weights of 1- and 2-year-old females increased from late winter to early summer ($P \leq 0.0001$ and $P = 0.003$, respectively). Means differed by 7.8 kg in 1-year-olds and 8.9 kg in 2-year-olds, representing gains of 43% and 27%, respectively, over late winter (Table 1). Unlike males, mean weights of non-lactating females 3–5 years old did not change from late winter to early summer, and females ≥ 6 years old gained, on average, 7.3 kg ($P = 0.06$). Mean weights of lactating females showed no significant trends.

Sample size in individual years was not sufficient to determine whether weight changes differed among years, but trends appeared to be consistent. Our largest sample was of yearling males ($n = 88$ weights); each year, this cohort showed increases of $\geq 30\%$ in mean weight between late winter and early summer. Similarly, female yearlings showed increases every year.

Weight Changes in Individual Bears

Most 1- to 2-year-old bears, both male and female, maintained or gained weight from late winter to late spring; from late spring to early summer, the tendency for individuals to gain, rather than simply maintain weight, was significant (males: $n = 14$, $P = 0.002$; females: $n = 7$, $P = 0.08$; Tables 2 and 3). Individuals gained up to an average of 0.1 kg/day over the entire period, and 0.3 kg/day during shorter spans (1–4 weeks).

Among males ≥ 3 years old, 6 of 7 gained weight from late winter to late spring; but between late spring and early summer, 9 of 14 lost weight. Some weight loss was rapid: one 3-year old lost an average of 0.9 kg/day between 30 May and 28 June and a 5-year old lost 0.5 kg/day over a 3-week period in June. Females 3–5 years old showed no discernable pattern. Older females (≥ 6 years) that were not lactating neither consistently gained nor lost weight from late winter to late spring, but they gained weight from late spring to early summer ($n = 8$, $P = 0.05$) and over the entire late winter to early summer period ($n = 15$, $P = 0.09$). In contrast, lactating females ≥ 6 years old all lost weight ($n = 11$, $P = 0.004$), averaging 0.2 kg/day (Table 3). One 19-year-old lactating female lost an average of 0.5 kg/day during late June, and a 14-year-old averaged 0.5 kg loss/day from 10 March–27 June, losing a total of 54 kg.

Growth in Stature

Young bears grew in stature as well as weight during the spring (Table 4). For 1- and 2-year-old males, in-

Table 1. Body weight of black bears by age, sex, and season in northcentral Minnesota, 1981–89

Sex	Age (yr)	Body weight (kg)								
		Late winter			Late spring			Early summer		
		3 Feb–31 Mar			11 May–7 Jun			8 Jun–15 Jul		
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	
Males	1	22.1	0.9	43	27.4 ^a	1.5	19	32.6 ^{a,b}	1.3	26
	2	40.8	2.6	7	49.5	3.8	18	54.9 ^{a,b}	1.9	32
	3	63.8	4.2	9	71.1	3.9	14	70.1	2.5	21
	4	84.8	5.1	11	106.2 ^a	6.4	9	86.0 ^a	5.3	11
	5	114.5	9.0	7	124.7	11.9	7	99.3 ^a	6.3	5
	≥6	145.5	4.9	22	136.0	5.0	11	129.7 ^b	4.5	21
Non-lactating females	1	18.1	0.8	44	21.0 ^a	1.9	8	25.9 ^{a,b}	1.6	9
	2	33.4	1.8	13	40.0 ^a	1.4	8	42.3 ^b	1.8	12
	3	46.2	2.1	9	52.5	2.3	14	51.8	1.9	14
	4	58.0	2.5	7	59.6	4.9	5	59.5	1.5	8
	5	65.4	9.1	5	69.1	8.2	2	63.4	3.7	6
	≥6	66.3	2.2	35	74.6 ^a	2.8	19	73.6 ^b	3.2	24
Lactating females	3	58.6		1				51.8		1
	4	66.2	3.0	7				56.9	3.2	4
	5	67.4	3.4	11	59.4	4.4	3	66.4		1
	≥6	81.6	3.0	39	77.1	4.5	3	74.7	2.8	15

^a Mean differed significantly from mean in previous season, $P \leq 0.1$; statistical-comparisons used log-transformed data.

^b Early summer differed from late winter, $P \leq 0.1$.

creased mean head length from late winter to early summer represented 68% and 91%, respectively, of the average growth from 1 year to the next. In 1- and 2-year-old females, 44% and 47%, respectively, of the year's growth occurred before early summer. Head

length reached about 95% of full size by early summer at age 3 in females and by age 5 in males (Table 4).

Increased weight and skeletal growth were often not accompanied by increased chest girth. Among 13 male yearlings measured in late winter and again during May

Table 2. Numbers of bears showing increases, decreases, or no change^a in weight between late winter, late spring, and early summer, northcentral Minnesota, 1981–89.

Sex	Age (yr)	Late winter–late spring			Late spring–early summer			Late winter–early summer		
		Increase	Decrease	No change	Increase	Decrease	No change	Increase	Decrease	No change
Males	1–2	5	1	4	13 ^b		1	9 ^b		
	3	1			1	7		2		
	4–5	4	1		2	1	1	3 ^b		1
	≥6	1			1	1		3	2	
Non-lactating females	1–2	2	2	3	5 ^b	1	1	3		1
	3	2			2	2	1	3		
	4–5	3	1			1	2	2	2	1
	≥6	5	4	3	5 ^b		3	11 ^b	3	1
Lactating females	3								1	
	4–5		3		1	1			3	1
	≥6		3			2			11 ^b	

^a Change defined as ≥ 1 kg.

^b Change significant at $P \leq 0.1$

Table 3. Median daily rates of weight change estimated from sequential weighings of black bears in late winter, late spring, and early summer, northcentral Minnesota, 1981–89.

Sex	Age (yr)	Net daily rate of change (kg/day) ^a					
		Late winter–late spring		Late spring–early summer		Late winter–early summer	
		Median	n	Median	n	Median	n
Males	1–2	0.01	10	0.20	14	0.05	9
	3	0.31	1	-0.16	8	0.03	2
	4–5	0.04	5	0.10	4	0.07	4
	≥6	0.11	1	-0.17	2	0.06	5
Non-lactating females	1–2	0.00	7	0.14	7	0.06	4
	3	0.10	2	0.00	5	0.04	3
	4–5	0.02	4	-0.01	3	0.01	5
	≥6	0.01	12	0.16	8	0.04	15
Lactating females	3					-0.06	1
	4–5	-0.09	3	0.16	2	-0.03	4
	≥6	-0.28	3	-0.29	2	-0.24	11

^a (Second weight - first weight)/(days between weighings)

or June, 10 gained ≥1 kg and 12 increased in head length by ≥1 cm, but 9 decreased in chest girth (mean changes: 3.8 kg weight gain, 2.3 cm increased head length, 3.7 cm loss in chest girth). Among 8 female yearlings, 6 increased in weight and all increased in head length, but all decreased in girth (mean changes: 2.9 kg weight gain, 2.3 cm increased head length, 7.3 cm loss in girth). Among 16 adult males and females ≥6 years old that gained weight during the spring, 2 increased in girth, 3

showed no change and 11 lost ≥2 cm (mean changes: 6.8 kg weight gain, 3.8 cm loss in girth.)

Bears with Supplemental Food

Thirty-five bears were known to visit garbage dumps in the spring or to consume baits at ≥3 trap sites. These bears generally were heavier than those that did not consume bait or visit dumps. Yearlings with access to dumps or baits averaged 8.3–15.4 kg heavier than yearlings of

Table 4. Head length in black bears by age, sex, and season in northcentral Minnesota, 1981–89.

Sex	Age (yr)	Head length ^a (cm)								
		Late winter			Late spring			Early summer		
		7 Feb–31 Mar			11 May–7 Jun			8 June–15 Jul		
		\bar{x}	SE	n	\bar{x}	SE	n	\bar{x}	SE	n
M	1	24.4	0.2	44	25.5	0.9	19	27.8	0.6	25
	2	29.4	0.5	7	30.0	0.5	19	31.5	0.2	32
	3	31.7	0.5	9	32.4	0.4	14	33.7	0.4	19
	4	34.5	0.5	11	35.3	0.6	9	35.0	0.5	11
	5	36.0	0.8	7	36.3	0.8	7	35.8	0.7	5
	≥6	37.0	0.4	22	36.2	0.4	11	37.5	0.3	22
F	1	23.3	0.3	43	23.8	0.8	9	25.7	0.4	7
	2	28.7	0.8	14	28.4	0.3	9	29.5	0.5	12
	3	30.4	0.4	10	31.2	0.4	14	31.6	0.3	14
	4	32.0	0.3	14	31.7	0.9	6	31.6	0.5	11
	5	32.5	0.3	16	33.0	0.8	4	31.7	0.7	6
	≥6	32.7	0.2	76	33.4	0.3	22	32.7	0.3	39

^a Measured to the nearest cm from tip of nose to intersection of lambdoidal and sagittal crests.

the same sex and in the same season that did not use supplemental foods (19 of 20 exceeded non-dump average weight). Among 1- to 2-year-old bears with sequential weights, median rates of gain from late winter to late spring were 10 times higher for 4 that visited dumps (0.1 kg/day) than 17 that did not (0.01 kg/day). However, we discerned no difference between the 2 groups in rates of gain from late spring to early summer (0.16 kg/day for 17 dump bears versus 0.18 kg/day for 21 non-dump bears). The only adult male and 1 of 2 lactating females that visited dumps and were weighed in successive seasons lost weight during spring, despite access to human foods.

DISCUSSION

Sex–Age Differences in Spring Weight Changes

Young black bears in northcentral Minnesota gained weight and achieved much of the year's growth in stature during the spring. Older (≥ 6 years), non-lactating females also gained weight, though not as much or as consistently as 1- to 2-year olds, whereas adult males and lactating females tended to lose weight.

A potential problem in making these comparisons was that late spring and early summer weights may have included ingested food, whereas the digestive tracts of denned bears were empty (C. Robbins, Wash. State Univ., Pullman, pers. commun.). Thus, increased weight between denning and early summer could have reflected filling of the gut, not increased body mass. We do not believe this confounded our results significantly. We weighed gut contents from 6 hunter-killed bears during the fall and found that they averaged 4.5% of body weight (range 3–8%, SE = 0.9); however, much of the gut content was intestinal fluid, which was part of the bear's general body mass, rather than additional weight from ingested food. Moreover, retention rate for ingested food averages 7–13 hours in black bears (Pritchard and Robbins 1990), and our data indicated that most of the bears we weighed during late spring and early summer had been in traps >13 hours and most had defecated, indicating at least partial emptying of the gut after capture. About 61% of bears consumed baits after capture, which could have added up to 0.4 kg to their weight.

Underestimation of weight gains after den emergence was potentially more problematic. Late winter weights were obtained from bears 3–8 weeks before den emergence, so weight loss occurred between the time bears were weighed and when they started foraging in the spring. Based on pairs of weights from individual bears

handled in both December and February–March of the same winter, weight loss in the den averaged 0.14% of body weight/day for non-lactating bears ($n = 75$, SE = 0.006) and 0.24%/day for lactating females ($n = 25$, SE = 0.008). Extrapolating these rates of loss to approximate den emergence dates would yield weights 3–5% lower than the den weights used in our analyses; thus, observed weight gains between late winter and late spring were underestimated (and weight losses overestimated) by at least that amount.

Sex–age specific differences in weight change were likely related to 2 factors: (1) attainment of adult stature, and (2) reproductive status. Female black bears (Beecham and Rohlman 1994) and grizzly bears (*U. arctos*; Glenn 1980, Kingsley et al. 1988) complete most bone growth by puberty, which in northcentral Minnesota generally occurs at 3–4 years old (median = 3.8; Garshelis et al. 1998). In contrast, males continue to grow for several years after sexual maturity (Graber 1981, Kingsley et al. 1988), with most skeletal growth completed by 6–8 years of age (Rausch 1961, Alt 1980, Graber 1981, Beecham and Rohlman 1994).

In this study, those classes of bears that gained the most weight between late winter and early summer were still growing in stature (1- to 3-year-old males and 1- to 2-year-old females), as were 4- to 5-year-old males, who showed large gains from denning through late spring. Decreased girth concurrent with skeletal growth suggested that these bears continued to deplete fat stores after hibernation, presumably to fuel growth in bone and muscle tissue. Early spring plant foods may be rich in protein, but they are typically low in carbohydrates and fats (Landers et al. 1979, Mealey 1980, Pritchard and Robbins 1990); protein in newly emergent aspen leaves (a common food of Minnesota bears in spring) can approach 40% (Minn. Dep. Nat. Resour. unpubl. data). However, for growth, bears also require lipids and energy. Ingested protein can be catabolized for energy and used for lipid synthesis, but only at the expense of amino acids that could otherwise be cycled directly into body protein, if other sources of triglycerides and energy were available (Tortora and Anagnostakos 1978). Mobilization of body fat would make possible the most efficient use of ingested protein for growth. Harlow et al. (1990) reported that serum cortisol, which aids in the mobilization of fat for energy, remains high in black bears through the spring.

Many bears old enough to have completed most skeletal growth also gained weight during the spring. Like juveniles, these bears continued to deplete back fat as they increased mass of other tissues. Some growth in stature continues in bears after 6 years of age (Alt 1980, Graber

1981, Beecham and Rohlman 1994), and bears may need to rebuild tissue lost during the inactivity of hibernation (e.g., gut lining, muscle). Nelson et al. (1975) reported that lean muscle mass was preserved in captive bears during hibernation, but with updated data from the same facility, Koebel et al. (1991) found evidence of mild muscle atrophy in denning bears. Well-fed captive bears may show less loss of muscle mass during hibernation than wild bears that enter dens with lower fat reserves, particularly following a season of poor foods or several months of lactation. Atkinson et al. (1996) found that polar bears (*U. maritimus*) that started their summer fast in relatively lean condition derived a higher percent of their fasting energy from catabolism of lean body mass than fatter bears and suggested this was likely the case for ursids in general. Many wild adult bears probably need to rebuild muscle during the spring.

Spring forage can provide enough energy for bears to build bone and muscle, but bears apparently do not use this energy to replenish fat stores. Converting ingested protein to stored fat is energetically less efficient than converting it to body protein, because some of the available energy is lost when amino acids are deaminated and nitrogen excreted (Holter and Hayes 1977). Dietary protein may be scarce later in the summer, so it may make sense energetically to use amino acids efficiently when available and defer fat accumulation until foods rich in carbohydrate and fat are available. Moreover, the potential advantages of accumulating fat early in the year may not be worth the attendant energetic costs of carrying it (Robbins 1983); e.g., shedding fat in spring may help prevent overheating during hot weather, particularly with increased activity during the breeding season.

Breeding-related behavior and physiology may largely explain weight loss in breeding-age males. Around the start of breeding, many 3- to 5-year-old males, who were still growing in stature, lost weight. Late spring weight loss in adult male black bears has been reported in many studies (Jonkel and Cowan 1971, Beeman 1975, Pelchat 1979, Alt 1980, Graber 1981). Though some attributed this loss to the low quality of spring forage (Jonkel and Cowan 1971, Beeman 1975, Beecham and Rohlman 1994), others related it to increased energy expenditure, reduced food intake, or both, during breeding (Alt 1980, Graber 1981). Breeding males travel more extensively than non-breeders (Alt et al. 1980, Rogers 1987) and engage in agonistic interactions (LeCount 1982, Rogers 1987, Garshelis and Hellgren 1994). They also appear to curtail feeding. During the breeding season they use garbage dumps less (Herrero 1983, Rogers 1987, Garshelis 1989) they form a false annulus in tooth cementum, sug-

gesting food stress (Coy and Garshelis 1992) and they may have relatively low serum urea levels (Minn. Dep. Nat. Resour., unpubl. data), possibly indicating low ingestion rates (Corn and Warren 1985).

Elevated serum testosterone (Palmer et al. 1988, Garshelis and Hellgren 1994) also may have contributed to weight loss in breeding males. In Minnesota, serum testosterone in adult males remained low through early May, but then rose and peaked sharply in early June (Garshelis and Hellgren 1994) as breeding began. Testosterone administered to adult animals can cause direct, dose-related losses in fat and lean tissue (Hervey and Hervey 1981). In Minnesota, testosterone became elevated in males as young as 3 years, but serum concentrations were not as high as in older bears and returned to base levels sooner, often before the end of breeding (Garshelis and Hellgren 1994). This may explain why weight loss during breeding was not as consistent in 3-year olds as in older bears; sequential weighings of individual 3-year-old males indicated that most lost weight from late spring to early summer, whereas mean weights of bears in this age group increased during this period (Tables 1–3).

The only females that consistently lost weight in this study were those subject to the high energy demands of lactation. Weight changes in non-lactating females ≥ 3 years old were variable; ≥ 6 -year olds generally gained weight, whereas 3- to 5-year olds neither gained nor lost. Adults that raised cubs the previous summer were most likely to have entered dens in poor condition and lost the most lean body mass during hibernation. Weight gains of these older non-lactating females during spring thus may have reflected the rebuilding of muscle tissue. Weight changes in non-lactating adult females also may have been influenced by breeding. In many mammals, serum estrogen peaks just prior to ovulation (Baird 1984). Estrogen depresses growth and promotes fat loss (Hervey and Hervey 1981) which, combined with increased movements and activity during the breeding season (Alt et al. 1980, Rogers 1987), could cause estrus female black bears to lose weight. Progesterone, on the other hand, promotes weight gain (Hervey and Hervey 1981), and serum concentrations increase after conception in bears (Foresman and Daniel 1983, Harlow et al. 1990). Many females in this study likely had conceived by late June, so weight gains may have been influenced by progesterone.

Regional Variation in Spring Weight Changes

The spring weight gain exhibited by bears in northcentral Minnesota, compared to weight losses re-

ported in other areas, is difficult to explain. Across most of their range, including Minnesota, the spring diet of bears is similar, consisting almost entirely of young greens (Tisch 1961, Hatler 1972, Pelchat 1979, Rogers et al. 1988, Holcroft and Herrero 1991, DeBruyn 1992). The extensive use of ants by bears in northcentral Minnesota in June and early July (Garshelis et al. 1988) boosts fat intake (Redford and Dorea 1984; Minn. Dep. Nat. Resour., unpubl. data) and may result in higher rates of gain at that time than in areas where ants are not a major dietary component; however, consumption of ants in late spring is common in many places (Grenfell and Brody 1983, MacHutchon 1989, Raine and Kansas 1990, Holcroft and Herrero 1991, Hellgren 1993). The April–May diet of Minnesota bears would have provided *fewer* calories than diets in places where fish (Poelker and Hartwell 1973) or overwintered nuts (Graber and White 1983, Ternent 1995) or berries (Tisch 1961, Beecham and Rohlman 1994) were available to supplement greens or where elevation gradients enabled bears to follow receding snowlines and extend the period of feeding on succulent, high-protein forbs (Beecham and Rohlman 1994).

Possibly, bears in this study left dens in better condition than bears in parts of North America where they were reported to lose weight in spring. Yearling weights and reproductive parameters indicated that in some of these areas (e.g., Idaho, Beecham 1980; northeast Minnesota, Rogers 1987; Montana, Jonkel and Cowan 1971; and Tennessee, Beeman 1975) bears subsisted at a lower nutritional plane than in northcentral Minnesota (Garshelis 1994) and thus may have had less body fat remaining after denning to use as energy for growth during spring. However, this was not true in all areas where bears were reported to have lost weight during spring (e.g., Great Dismal Swamp, Hellgren et al. 1989). In places where the breeding season is longer than in Minnesota, or bears reach puberty at a younger age, breeding-related weight losses might be more evident; however, this should not affect weight changes in juvenile bears or changes early in the spring, because even where breeding extends later in the summer, it generally starts at about the same time as in Minnesota (Garshelis and Hellgren 1994). Possibly, our study bears made greater use of human-related food sources than in other areas. However, we were able to identify and eliminate bears that consumed garbage at dump sites. Though some bears could have obtained supplemental food near human dwellings (garbage, bird seed, etc.), many human dwellings in our study area were unoccupied until early summer, and few complaints of nuisance activity by bears around home sites occurred during the spring. Furthermore, if human-related foods

contributed significantly to the diet of study bears, we would have expected to see evidence in scats; instead, scats of trapped bears rarely contained human refuse, unlike scats collected at dumps (K. Noyce unpubl. data).

We suggest that some reported cases of spring weight loss from other areas likely were artifacts of data pooling and small sample size. Pooling 4- and 5-year-old males with older males (Pelchat 1979), lactating with non-lactating females (Jonkel and Cowan 1971, Pelchat 1979), 3-year-olds with either juveniles or adults (Hellgren et al. 1989), or bears weighed just after den emergence with those weighed in June (Alt 1980) could have confounded interpretations of spring weight change. In studies that lacked data from late winter (Jonkel and Cowan 1971, Blanchard 1987), only weight changes late in the spring (which were more likely to be influenced by breeding) were evaluated.

Several studies reported results similar to ours. In Yosemite National Park (Graber 1981), adult females and juveniles gained weight in spring on a diet of overwintered nuts. Bears gained weight during spring in Alberta feeding primarily on vetchling (*Lathyrus* spp.; Pelchat 1979), and in Colorado, on green plants and aspen buds (Beck, pers. commun., in Grenfell and Brody 1983).

Jonkel (1960) originally posited the negative foraging period in an unpublished progress report based on data from 4 bears. Eleven years (and many weighings) later, Jonkel and Cowan's (1971) published monograph presented data similar to ours, albeit with a somewhat higher incidence of weight loss in juveniles. Their juveniles and adult females generally gained weight from May to July; adult males gained from May to June and decreased only between June and July. They did not use the term negative foraging period in their monograph, but stated that "Bears of all age classes either gained weight slowly or lost weight during the spring and early summer" (Jonkel and Cowan 1971:45). Poelker and Hartwell (1973), without evidence of weight loss in their own study, referenced another early progress report of Jonkel's (1962) and resurrected the term negative foraging period. Later, Hellgren et al. (1989) used the phrase, despite a small sample in which only adult males showed a clear indication of weight loss. Both these papers based conclusions partly on declining condition indices (e.g., fat thickness, weight:length ratios). We found that bears often gained weight while their girth (condition) declined. Beecham and Rohlmann

(1994) cited evidence of the negative foraging period, even though Beecham's (1980) data showed more juveniles gaining than losing weight between late May and mid-July.

We believe the presumption of weight loss or stymied growth in the spring has become entrenched in the scientific literature on bears without adequate documentation. As a result, the significance of spring foods for the growth of young bears has been overlooked. Green vegetation is commonly assumed to be a food of necessity, not of choice for bears (Eagle and Pelton 1983, Rogers 1987). This may be true in late summer, when herbaceous material is less nutritious (Pritchard and Robbins 1990) and bears may lose weight in the absence of adequate fruits (Rogers 1987). However, during spring, plant foods are higher in protein and lower in fiber than later in the year (Tew 1970; Mealey 1980; Minn. Dep. Nat. Res., unpubl. data), and bears are only 5% less efficient at extracting plant protein than ruminants (Pritchard and Robbins 1990). Supplies of herbaceous foods are virtually unlimited by mid-spring. High water and cellulose content may mean that ingestion rate is the factor limiting nutritional gain from herbaceous foods. However, large volumes can be ingested in a short time, and bears increase their intake and gut passage rate when feeding on greens relative to other foods (Pritchard and Robbins 1990). It is significant to note that bears grow much of their new fur each year before mid-July; this physiologic function, like growth, requires protein intake above maintenance level and is often timed to match periods of high protein availability (Robbins 1983).

Bears may complement spring vegetation with carbohydrate- or fat-rich foods, but in another Minnesota study, where bears had access to abundant overwintered acorns, they still fed largely on greens (Ternent 1995), suggesting that vegetation was an important dietary component. Minnesota bears also fed on some herbaceous foods (e.g., jewelweed [*Impatiens* spp.] and wild calla) even after berries were available (Rogers et al. 1988), and in Yellowstone National Park, grizzly bears consumed clover throughout the summer (Mealey 1980, Mattson et al. 1991). These plant species all retain relatively high protein (>20%) and low fiber (<50%) as they mature (Minn. Dep. Nat. Resour., unpubl. data), and this protein may complement the energy-rich summer diet of berries and nuts. The need for dietary protein may decline in fall, as digestion shifts to favor fat and carbohydrate assimilation (Brody and Pelton 1988) and metabolism favors fat deposition (Nelson et al. 1983).

Hellgren et al. (1989) were puzzled by weight losses among bears in the Great Dismal Swamp on a spring diet

that was higher in protein and comparable in fat and fiber to foods in other seasons. Likewise, in their review of food habits of black bears across North America, McDonald and Fuller (1993:295) stated that "Protein rich foods are relatively abundant during spring, but bears do not seem to gain weight during this season." Uncritical acceptance of the notion of a negative foraging period has thus introduced an apparent paradox. Based on our study and a careful examination of the literature, we suggest that there is no paradox. Young bears can grow well on the protein supplied by spring foods.

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