

EFFECTS OF SPRING ACORN AVAILABILITY ON BLACK BEAR DIET, MILK COMPOSITION, AND CUB SURVIVAL

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We investigated the role of changing abundance of spring foods on female American black bear (*Ursus americanus*) diet, milk composition, and cub survival in western Massachusetts. We hypothesized that diets would change, percentage milk fat would be higher, and cub survival would be higher in a year when overwintered hard mast was more abundant. We obtained paired samples of milk from 7 adult female bears across consecutive reproductive cycles during which spring diets differed; 1 year followed a bumper acorn (*Quercus rubra*) crop and estimated spring diets were >25% acorns; the other year followed an extremely poor acorn crop and spring diets were estimated to be 99% skunk cabbage (*Symplocarpus foetidus*). Postdenning milk was higher in fat (26.7% versus 18.2%; $P = 0.0557$) during the spring when acorns were abundant, but we did not identify any carryover affect to cub survival. We suggest that adult female black bears compensate for changes in food availability by eating greater volumes of alternative foods, and perhaps allocate resources primarily to milk production; the bears appear to be able to produce milk of adequate quality to sustain cubs, regardless of spring diet.

Key words: black bear, cubs, fat, hard mast, Massachusetts, milk, *Quercus*, skunk cabbage, *Symplocarpus foetidus*, *Ursus americanus*

Demographic responses of carnivores to changes in food availability are often pronounced, and have been documented particularly well in species that depend on a limited array of food resources (Fuller and Sievert 2001). In addition to changes in age of 1st reproduction and pregnancy rates, changes in neonate survival often accompany changes in food availability; postpartum mortality of lynx (*Lynx lynx*—Brand and Keith 1979), wolves (*Canis lupus*—Fuller 1989), lions (*Panthera leo*—Van Orsdol et al. 1985), and wolverines (*Gulo gulo*—Landa et al. 1997) was negatively correlated with overall food abundance. These changes are believed to be a consequence of poorer adult condition (e.g., lower fat reserves—Brand and Keith 1979; Todd and Keith 1983) and, consequently, poorer nutrition of juveniles (e.g., Lindstrom 1983).

On the other hand, alternative food resources may compensate for changes in primary food availability (Fuller and Sievert 2001). The reproductive output of coyotes (*Canis latrans*) did not change in the face of a snowshoe hare (*Lepus americanus*) decline, where the coyotes used supplemental farm carrion as an alternative food source (Todd 1985).

Similarly, martens (*Martes americana*) maintained body condition in years when rodent prey was low by switching to alternate food sources (Ben-David et al. 1997). Omnivores would seem more likely to be able to mitigate major changes in food availability than dietary specialists.

An important supposition in food-related survival of neonate carnivores is that milk quality, and perhaps volume, is the ultimate factor that affects neonate condition. When food availability is low, milk should be “less nutritious” and juvenile growth slower (c.f., Lindstrom 1983; Messier 1987) than when food is abundant. For species that are able to switch to alternative food sources, either milk quality is maintained or, if milk composition changes, increased milk volume can compensate for its lower nutritional quality.

Pregnant black bear females give birth in dens and lactate for about 3 months while denning to feed newborns (Alt 1983, 1989). During this period, females do not eat or drink, but maintain a high body temperature (Folk et al. 1972) and may produce >25 kg of milk (Oftedal et al. 1993). This milk is high in fat (Oftedal et al. 1993) and derived from depot fat stores (Iverson and Oftedal 1992). The fat percentage of milk is relatively constant during the denning period (Farley and Robbins 1995; Oftedal et al. 1993), but after den emergence milk composition changes because milk is synthesized primarily from nutrients in the female’s diet (Iverson and Oftedal 1992; Iverson et al. 2001).

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Spring diets of black bears in the northeastern United States are typically composed of green vegetation (McDonald and Fuller 1994). However, bears will use overwintered hard mast (e.g., acorns) if it is available (Elowe 1984). Hard mast has higher fat content than green vegetation, which may be higher in protein. Because mast crops are variable, the composition of the spring diet changes annually (Costello et al. 2003). Farley and Robbins (1995) reported that about 90% of total cub milk consumption occurs after den emergence, and that milk intake by cubs in captivity rose steadily from about 70 days postpartum (around den emergence) to a peak at around 200 days postpartum. Because most cub mortality apparently occurs within the first 3 months after den emergence (Elowe and Dodge 1989; LeCount 1987), the composition of spring milk could influence black bear population dynamics by affecting cub growth and ultimately, survival. The mechanism affecting cub survival is presumed to be a lower nutritional plane in females, which subsequently affects milk quality, quantity, or the ability to lactate (Costello et al. 2003; Eiler et al. 1989; Elowe and Dodge 1989). However, black bears are dietary generalists, and lactating females likely compensate for changes in acorn availability by consuming greater quantities of foods with lower fat content, and thus minimizing the effect of spring food on cub survival. Indeed, Kasbohm et al. (1996) did not document any effects of mast failure caused by gypsy moth (*Lymantria dispar*) defoliation on cub survival to 1 year in Virginia.

Our objectives in this study were to determine the composition of milk from a sample of free-ranging black bears, both in dens and postdenning, over consecutive reproductive cycles when food availability, and thus diet, changed significantly. Our underlying assumption, based on the literature, was that spring diet quality was positively related to the amount of hard mast that bears consumed. We believe this is the 1st report of the direct effects of spring diet on milk composition in free-ranging black bears. Other reports on black bear milk composition either did not measure changes in milk in the same bears at different stages of lactation, or used captive bears (Farley and Robbins 1995; Iverson and Oftedal 1992; Oftedal et al. 1993). Also, no researchers that reported on milk composition directly estimated diets of free-ranging bears or collected milk samples from the same bears exposed to different food availabilities over time.

Our hypotheses were that estimated spring bear diets would differ between years with differing food availability, that there would be no differences in gross milk composition during the denning period in a sample of bears followed over consecutive reproductive cycles, that bears consuming high fat diets during spring would have a greater milk fat content than bears consuming low fat diets, and that cub survival would be lower during a year when spring milk fat percentage was low than during a year when spring milk fat percentage was high.

MATERIALS AND METHODS

Study area.—We collected data in western Massachusetts (42°27'N, 72°41'W) on the 150-km² Conway–Williamsburg Study Area. The study area is 70% forested and >90% privately owned; elevations range from 30 to 450 m (Fuller 1993). Hardwood-dominated forests

consisted of northern red oak (*Quercus rubra*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), black birch (*Betula lenta*), sugar maple (*A. saccharum*), and hickories (*Carya*). Major softwoods were eastern white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*).

The major agricultural crop present in the study area, and used by bears, was feed corn for dairy cattle. Between 10 and 20 cornfields (0.4–4.0 ha) were present in the study area each year. Other human-related food sources included apiaries, apple orchards, and home bird feeders. Human densities in the study area ranged from about 18 to 459/km² (Horner 1996).

Food availability.—We estimated hard mast abundance in autumn by using 2 methods: visual estimates along transects and seed traps. We established 12 line-transects (0.5 km) with stations at 100-m intervals in hardwood stands in the study area. We selected stands randomly from among those large enough to have a 0.5-km transect remain entirely within a hardwood-dominated area. This biased estimates to some degree because we also observed that bears fed in hardwood stands that were too small to be selected for most surveys, especially hickory stands. We selected the nearest mast-producing tree (oak, hickory, or American beech) in each quarter (N, E, S, W), within 17.8 m of the sample point (0.10-ha circle) for evaluation. We subjectively ranked relative mast production in 4 categories: none or almost none (0), low abundance (1), abundant (2), and extremely abundant (3). A single observer (JEM) surveyed all transects during late August–early September 1993–1995.

We randomly selected 4 transects for seed trap placement. We placed 2 traps at each station under the crown of ≥ 1 tree (some large crowns overlapped) for which a visual estimate of mast production was obtained. Seed traps were 0.5-m² circular hoops fitted with a clear plastic tube tied shut at the bottom to allow water to drain but mast to be retained (Christisen and Kearby 1984). We set out traps when mast surveys were conducted and checked them at 2-week intervals until the end of mast fall. We sorted mast according to species, removed caps and shells, assessed each item for soundness (e.g., whether insects had already consumed nut tissue), oven-dried sound mast to a constant weight, and weighed it to the nearest 0.1 g. We estimated annual mast production (kg dry mass/ha) by pooling for each station and transect the entire mast collection in a season.

We assigned mast species to 3 groups: northern red oak, American beech, and other species. Northern red oak was the dominant mast-producing tree species in the study area, comprising about 22% of all dominant and codominant trees (Fuller 1993). Northern red oak acorns overwinter before germination (Harlow et al. 1979) and are available when bears emerge from dens. American beech was the 2nd most abundant mast-producing species in the study area, and several other species of oak and hickory were present in low abundance (Fuller 1993). We did not include an assessment of soft mast (e.g., fruit such as blueberries [*Vaccinium*], and cherries [*Prunus*]) abundance because it would not overwinter.

We resurveyed the same transects that had seed traps during April–May (depending on snow melt), in 1994 and 1996, to estimate the amount of residual hard mast. At each station we established 1-m² plots 2 m from the sample point in each of the cardinal directions. We collected hard mast on the ground (litter searched down to mineral soil), assessed each item for soundness, and oven-dried and weighed it as above. Because of the variable nature of mast crops, we anticipated observing differences in autumn, and thus spring, food availability and concomitant changes in bear diets in spring.

We made no attempt to quantify the abundance of skunk cabbage during any year or season. Skunk cabbage occurred in most wet areas

throughout the study area, in large patches covering >1 ha in wetlands and in small patches of a few plants along the borders of streams and spring seeps. We visited the same areas each year to search for scats and to capture bears; based on our qualitative appraisals, skunk cabbage abundance and distribution did not appear to vary among years.

Food use.—We collected bear scats opportunistically during food surveys and radiotracking during spring (April–June) 1994 and 1996. We also searched for scats at black bear locations estimated from radiotracking, 1–14 days after the locations were recorded. Scats were frozen until analyzed. We removed debris from and recorded the volume of frozen scats via water displacement to the nearest 10 ml. We thawed and washed scats through a series of sieves (Hatler 1972), identified scat contents, and estimated the volume of each item in a scat. We classified scat contents into major food types: skunk cabbage, grass or sedge, other vegetation, soft mast, corn, oak mast, other hard mast, mammal remains, and other animal remains. We pooled the food-type volumes estimated from individual scats into a single volume measure for each spring to estimate percentage diet composition; thus, we do not present food use data as mean \pm SE, but as a composite percentage.

We derived diet profiles from scat analysis and used nutritional values for food groups in Kasbohm (1994) to calculate percentage protein and percentage fat in black bear spring diets, except for skunk cabbage and red oak acorns. We estimated skunk cabbage and spring red oak composition directly from samples taken in the study area (Iverson et al. 2001). We weighted reported composition values for various foods or food groups by the percentage volume in bear scats, and combined them to develop nutritional profiles of bear diets (Hellgren et al. 1989). We realize that these estimates are from the nutritional composition of the feces and differential digestion among food types was likely. We did not correct scat-estimated diets for digestibility because there was no available correction factor for skunk cabbage, the major spring food, and we did not have the resources (i.e., captive bears) to develop a correction factor.

Bear data and milk samples.—Black bears normally give birth (and thus lactate) on a 2-year cycle if they are successful in rearing ≥ 1 cub. Fortunately, we had previously captured and then were able to sample many of the same individual females over 2 consecutive litter cycles (1994 and 1996 for this study). We captured free-ranging female bears during 1992–1997 by using foot snares, trained bear hounds, and in dens, and fit or refit adult and yearling females with radiocollars (ATS, Inc., Isanti, Minnesota). Some bears were initially captured and radiocollared during earlier research projects (Elowe 1984; Fuller 1993) dating to 1981. We immobilized bears by using a mixture of ketamine hydrochloride (10–17 mg/kg body mass) and xylazine hydrochloride (1–2 mg/kg) or tiletamine hydrochloride (3.9–7.3 mg/kg). Ketamine (6–10 mg/kg) alone was sometimes used on small bears (<50 kg). Our capture and handling conformed to procedures that were later incorporated as part of the animal care and use guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

We weighed bears with spring scales to the nearest 0.46 kg. We used the mass-loss equation reported in Samson and Huot (1995) to standardize masses of lactating females to parturition masses (late December mass = $9.41 + 2.16[\text{litter mass}] + 0.96[\text{late winter mass}]$; all masses in kg).

We obtained milk samples from female bears with new cubs in winter dens during late February and March (6–8 weeks postpartum; we estimated mean birth date of litters at around 20 January each year based on hair length—Alt 1989). We then recaptured the same females during late May and early June (17 May–2 June 1994; 19 May–6 June 1996) by using either trained bear hounds or by stalking and darting

TABLE 1.—Estimated dry mass (kg/ha) of available hard mast produced by several tree species on the Conway–Williamsburg Study Area in western Massachusetts, 1993–1996. Values given are $\bar{X} \pm SD$.

Season	Year	Red oak	Beech	Other ^a
Autumn	1993	508.4 \pm 769.0	1.3 \pm 1.4	11.0 \pm 14.9
	1995	7.6 \pm 11.2	0.4 \pm 0.4	0.0 \pm 0.0
Spring	1994	395.5 \pm 454.1	0.5 \pm 0.3	19.8 \pm 32.6
	1996	0.9 \pm 1.3	0.0 \pm 0.0	0.1 \pm <0.1

^a Includes chestnut oak (*Quercus prinus*), black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), and shagbark hickory (*Carya ovata*).

females on the ground (McDonald 2003). In both seasons we used oxytocin (20–60 IU), injected intramuscularly, to facilitate milk letdown. We manually expressed milk from each teat but may not have completely evacuated all milk present. We could not determine time since last suckling. We collected 5–20 ml of milk and stored it frozen until analyzed. All females from which we obtained paired milk samples (in-dens and postdenning) were adults that had already had ≥ 1 litter before 1994.

We did not radiomark neonate cubs to assess survival. Rather, we estimated minimum 1st-year survival by visiting dens of individual females in consecutive years, because cubs normally den with their mother as yearlings (McDonald and Fuller 1998). Cubs observed in natal dens and not present in dens with females as yearlings were assumed to have died. Females with yearlings sometimes abandoned dens when approached. If there was snow cover, we tracked bears until the number of yearlings could be determined. Alternatively, we made subsequent den visits to get an accurate count of yearlings or stalked family groups shortly after den emergence.

Milk composition.—Milk samples were thawed at room temperature or in a warm water bath and duplicate aliquots (about 0.5 g) from all samples were analyzed. After samples were thawed and homogenized, milk lipid was extracted into chloroform by using a modification to the method of Folch et al. (1957). Dry matter and protein were analyzed in duplicate by using forced convection drying and macro-Kjeldahl methods, respectively. All glass containers, caps, and instruments were lined with Teflon. Samples were weighed with an analytical scale to 0.1 mg and percentage milk lipid was calculated as the total weight of purified lipid divided by total mass of the sample (Iverson et al. 2001).

Statistical analyses.—We compared gross composition of black bear milk samples taken from individual bears in winter dens and in late spring by using paired *t*-tests. We also used paired *t*-tests to compare in-dens and late-spring milk samples for individual bears between litter cycles. We compared mean daily body mass change (in-dens mass versus postdenning mass; kg/day) for females between years with *t*-tests. We used Fisher's exact test to compare minimum 1st-year survival between years (Zar 1996). We used $\alpha = 0.10$ for all tests.

RESULTS

The estimated dry weight (kg/ha) of northern red oak mast produced was greater during autumn 1993 than autumn 1995 (Table 1). Thus, the amount of overwintered red oak mast available in spring 1994 was greater than in spring 1996 (Table 1). American beech mast production also differed between autumn 1993 and autumn 1995; we did not find any viable beechnuts in spring 1996 samples (Table 1). Other species of mast, mostly oaks, were more abundant in spring 1994 than in

TABLE 2.—Spring (April–June) black bear diet composition (% volume) in western Massachusetts during 1994 ($n = 107$) and 1996 ($n = 71$), as estimated from scat analysis.^a

Food	1994	1996
Skunk cabbage	52.2	99.3
Oak mast	27.4	
Grass or sedge	7.6	
Unidentified plant	10.3	<1.0
Fruit	1.1	
Corn	<1.0	
Mammal remains	1.0	<1.0
Other animal	<1.0	

^a Total volume of food items in all n scats/total volume of all scats.

spring 1996; we did not find any viable nuts of these species during autumn 1995 seed-trap sampling (Table 1). The lack of viable nuts of any species in most seed traps during autumn 1995 and spring 1996 precluded statistical analyses.

We estimated that skunk cabbage made up 52.2% of the spring 1994 diet after the excellent hard mast year of 1993 and 99.3% of the diet during spring 1996 after the poor mast year in 1995 (Table 2). Oak mast comprised 27.4% of the spring 1994 estimated diet and was not detected in any scats during spring 1996 (Table 2). We estimated that spring dietary protein was 7.01% for 1994 and 3.18% for 1996 and spring dietary fat was 4.09% in 1994 and 0.93% in 1996. These fat estimates are lower than those reported elsewhere (e.g., 4.8–15.2% uncorrected for digestibility in Kasbohm [1994]) but are based on our estimates of fat in skunk cabbage (0.80%) and red oak acorn meats (8.94%) from spring samples collected in the study area (Iverson et al. 2001).

We did not detect a difference in estimated late December masses of female bears between years (paired $t = 0.0467$, $d.f. = 4$, $P = 0.9646$), or in mean mass change between in-den and postdenning samples (-0.148 kg/day in 1994 versus -0.141 kg/day in 1996; paired $t = 0.432$, $d.f. = 4$, $P = 0.6835$). Rates of mass change from in-den to postdenning samples ranged from -0.253 kg/day to 0.006 kg/day. Only 1 female, in 1996, of all those sampled in both years, gained mass between the in-den and postdenning samples.

We obtained paired samples for denning and postdenning milk from 10 bears in 1994 and 8 bears in 1996. This also constituted paired denning milk samples from 8 bears across years and paired postdenning samples from 7 bears across

TABLE 3.—Composition (%) of milk from 7 individual postparturient black bears in western Massachusetts. Samples were obtained from each bear in dens and 1.5–2 months after den emergence during both 1994 and 1996. Values given are $\bar{X} \pm SD$.^a

Component	In-den		Postdenning	
	1994	1996	1994	1996
Dry matter	33.3 \pm 3.1	34.1 \pm 1.9	42.4 \pm 5.9	34.8 \pm 4.7
Protein	6.6 \pm 0.6 A	7.1 \pm 0.6 A	7.9 \pm 0.6 B	9.0 \pm 1.2 C
Fat	21.8 \pm 7.8 A	18.2 \pm 1.5 A	26.7 \pm 6.9 B	18.2 \pm 5.8 A

^a Means with a different letter within a row are statistically different (paired t -test; $P < 0.10$).

TABLE 4.—Minimum 1st-year survival of black bear cubs of females that had in-den and postdenning pairs of milk samples collected in western Massachusetts in both 1994 and 1996.

Year	No. litters	No. cubs	No. cubs that lived ^a	Minimum cub survival rate
1994 ^b	7 (8)	18 (21)	13 (16)	0.72 (0.76)
1996 ^c	7 (6)	17 (15)	13 (13)	0.76 (0.87)

^a Present in den with mother as yearlings in year $n + 1$.

^b Numbers in parentheses include litter of bear 42, which was killed during the 1996 fall hunting season.

^c Numbers in parentheses exclude litter of bear 75, which was not lactating when captured on 2 June 1996; because she had new cubs in her winter den in 1997, we assumed her 1996 litter of 2 was lost before 2 June.

years. Iverson et al. (2001) provided detailed profiles of the fatty acid composition of the milks of these bears.

Various aspects of milk composition differed between seasons within years and between years. Postdenning fat was greater than in-den fat in 1994 (paired $t = 2.395$, $d.f. = 8$, $P = 0.0402$; Table 3) but not in 1996 (paired $t = 0.485$, $d.f. = 6$, $P = 0.6424$; Table 3). Postdenning fat differed between years (paired $t = 2.367$, $d.f. = 5$, $P = 0.0557$; Table 3) but in-den fat did not (paired $t = 1.155$, $d.f. = 6$, $P = 0.2870$; Table 3). Milk protein differed between in-den and postdenning samples each year (1994: paired $t = 2.813$, $d.f. = 8$, $P = 0.0203$; 1996: paired $t = 3.541$, $d.f. = 6$, $P = 0.0095$; Table 3) and between 1994 and 1996 postdenning samples (paired $t = 3.077$, $d.f. = 5$, $P = 0.0218$; Table 3).

Minimum 1st-year survival of cubs born to monitored female bears did not differ between years (Fisher's exact test, $P = 0.927$; Table 4). Inclusion or exclusion of data from individual bears for which complete information from both years was not possible did not affect this conclusion (Fisher's exact test, $P = 0.654$; Table 4).

DISCUSSION

In our study area, skunk cabbage was widespread and predictably abundant each year but hard mast crops varied unpredictably. We detected differences in postdenning composition of milk between years when bears had different spring diets due to variation in food availability. Bears had a higher spring milk fat percentage during a year when they fed heavily on overwintered hard mast. We did not detect differences in denning-period milk composition (i.e., from fasting bears) between years even though we documented differences in autumn diets in which bears increased their use of several alternate foods, especially corn, when mast crops were low (McDonald and Fuller 2001).

Our estimates of milk composition were comparable to those reported elsewhere (Farley and Robbins 1995; Jenness et al. 1972; Oftedal et al. 1993), except that postdenning protein levels were about 50% lower than those reported for captive black bears (Farley and Robbins 1995). However, Farley and Robbins (1995) reported that protein levels increased markedly between 100 and 150 days postpartum, around the time we collected our postdenning samples. Jenness et al. (1972)

reported high protein levels from 4 samples collected during August. Because we did not collect milk samples during late lactation (summer), we simply may not have observed further increases in milk protein.

The trends we observed in 1994 in changes in milk composition from denning to postdenning samples (increased fat, protein, and dry matter) conformed to those expected based on previous studies (Jenness et al. 1972; Oftedal et al. 1993). The same trend in increasing milk solids during lactation has been observed in captive black bears (Farley and Robbins 1995), northern elephant seals (*Mirounga angustirostris*—Reidman and Ortiz 1979), and Tammar wallabies (*Macropus eugenii*—Green et al. 1983). In polar bears (*Ursus maritimus*), because their lactation cycle is longer, trends in milk solids vary over the course of lactation according to the female's activity (Derocher et al. 1993).

We did not detect a difference in the rates of postdenning weight loss for lactating adult females between years, although during a year when females had a low-fat diet one might have hypothesized that they would lose weight more rapidly after den emergence than in a year with a higher fat diet. Estimated weights at den entry and late winter were about the same for individual females in both years. The female that gained weight from the in-den to postdenning sample spent much time in wetlands among a series of housing developments, perhaps consuming human-related foods (e.g., sunflower seeds from bird feeders). However, this female had the lowest individual milk fat level (11.35%) in the paired sample and had milk with very high levels of 18:3n-3 fatty acid (Iverson et al. 2001), which is characteristic of green, leafy vegetation and thus consistent with a diet of skunk cabbage.

Skunk cabbage produced reliable and abundant forage annually. Skunk cabbage grows in dense stands, sometimes over extensive areas of wetland (Knutson 1979). Thus, bears were able to consume large quantities of skunk cabbage with little effort expended in foraging. Wetland areas also provided security for females with cubs. We often located bedding sites in wetland areas during spring; they were typically surrounded by large numbers of scats, indicating that individual bears spent considerable amounts of time in the vicinity. Bears could thus substitute quantity of food for quality when spring hard mast was scarce. Milk and milk fat are also synthesized from dietary protein and carbohydrates, and increased food consumption may have compensated for low direct availability of higher-fat foods.

All females in the study were adults (1 female was 4 years old during 1994, all others were older; also, we have no evidence that age of female was related to cub survival in western Massachusetts [McDonald 1998]) and had likely ceased structural growth (Noyce and Garshelis 1994). Thus, any calories consumed above metabolic maintenance would have been available for replenishing lost fat stores. Female bears in this study may have allocated extra dietary fat (e.g., in 1994) to milk production, perhaps at the expense of their own body condition. However, it is not clear that body fat accumulation is the optimal strategy for female bears during spring and early summer (Noyce and Garshelis 1998); thus,

there may not be a real cost to adult females of allocating dietary fat to milk production. Iverson et al. (2001) reported on changes in fatty acid composition of the milk of these bears. The fatty acid profiles of the milks closely corresponded with estimated fatty acid profiles of bear diets based on the scats we collected, thus we do not think that residual body fat stores contributed much to postdenning milk composition.

We did not capture cubs when obtaining postdenning milk samples (most sought refuge high in trees); thus we could not determine if growth rates differed between years. Our results suggest that adult females can maintain a baseline milk fat level, comparable to that produced while denning, even on a very low-fat diet (about 1%). If cub survival is related to growth rate, our results suggest that in-den milk fat levels (about 18%), if sustained during the postdenning period, can provide for adequate growth rates.

Black bear cubs are not exposed to the same cold environment after den emergence that polar bear cubs or seal pups are; thus they do not have the extreme need to accumulate body fat for thermoregulation. Because cubs are growing structurally during their 1st year, especially during the 1st few months after den emergence, protein may be more important than fat to growth. In 1996, when skunk cabbage made up most of the spring diets of bears, we observed relatively high levels of protein in post-denning milk even though our estimated dietary protein was lower than in 1994.

Our study of individual adult female bears in years of greatly contrasting hard mast availability did show differences in milk composition, but not in cub survival. We think survival of cubs born to multiparous females may be relatively immune to the effects of mast failures. The effects of spring food availability may be more pronounced on primiparous bears that must choose between their own structural growth and lactation; however, we have no data on milk composition from young bears producing their 1st litters. Adult female black bears appear to be able to produce milk of adequate quality to sustain cubs even when spring diets are poor.

ACKNOWLEDGMENTS

S. J. Iverson (Dalhousie University, Halifax, Nova Scotia, Canada) performed all milk and food item composition analyses. W. Woytek assisted with bear captures in both winter and spring; E. Howard, A. Howard, P. Glazier, and D. Glazier also assisted with bear capture. D. Luke and T. Russell provided bear hounds when necessary. K. McCarthy collected bear scats and helped with mast analyses. V. Carter, S. Schulman, and S. Powell analyzed scats. The manuscript was much improved by the comments and ideas of K. Noyce and 2 anonymous reviewers. The Cooperative Wildlife Research Lab, Southern Illinois University, Carbondale, allowed the senior author time to work on the manuscript. The Massachusetts Cooperative Fish and Wildlife Research Unit and the Department of Natural Resources Conservation at the University of Massachusetts, Amherst, provided logistical support and equipment. Bear capture and handling methods were approved by the University of Massachusetts Institutional Animal Care and Use Committee (protocol 15-02-02). The Massachusetts Division of Fisheries and Wildlife provided the senior author time to work on the project and funded the research through Federal Aid in Wildlife Restoration Project W-35-R.

LITERATURE CITED

- ALT, G. L. 1983. Timing of parturition of black bears (*Ursus americanus*) in northeastern Pennsylvania. *Journal of Mammalogy* 64:305–307.
- ALT, G. L. 1989. Reproductive biology of female black bears and early growth and development of cubs in northeastern Pennsylvania. Ph.D. dissertation, West Virginia University, Morgantown.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BEN-DAVID, M., R. W. FLYNN, AND D. M. SCHELL. 1997. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111:280–291.
- BRAND, C. J., AND L. B. KEITH. 1979. Lynx demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management* 43:827–849.
- CHRISTISEN, D. M., AND W. H. KEARBY. 1984. Mast measurement and production in Missouri (with special reference to acorns). Missouri Department of Conservation, Jefferson City, Terrestrial Series 13:1–34.
- COSTELLO, C. M., D. E. JONES, R. M. INMAN, K. H. INMAN, B. C. THOMPSON, AND H. B. QUIGLEY. 2003. Relationship of variable mast production to American black bear reproductive parameters in New Mexico. *Ursus* 14:1–16.
- DEROCHER, A. E., D. ANDRIASHEK, AND J. P. Y. ARNOULD. 1993. Aspects of milk composition and lactation in polar bears. *Canadian Journal of Zoology* 71:561–567.
- EILER, J. H., W. G. WATHEN, AND M. R. PELTON. 1989. Reproduction in black bears in the southern Appalachian Mountains. *Journal of Wildlife Management* 53:353–360.
- ELOWE, K. D. 1984. Home range, movements, and habitat preferences of black bears (*Ursus americanus*) in western Massachusetts. M.S. thesis, University of Massachusetts, Amherst.
- ELOWE, K. D., AND W. E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management* 53:962–968.
- FARLEY, S. D., AND C. T. ROBBINS. 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Canadian Journal of Zoology* 73:2216–2222.
- FOLCH, J., M. LEES, AND G. H. SLOANE-STANLEY. 1957. A simple method for the isolation and purification of total lipids from animal tissues. *Journal of Biological Chemistry* 226:497–509.
- FOLK, G. E., JR., M. A. FOLK, AND J. G. MINOR. 1972. Physiological condition of three species of bears in winter dens. *International Conference on Bear Research and Management* 2:107–125.
- FULLER, D. P. 1993. Black bear population dynamics in western Massachusetts. M.S. thesis, University of Massachusetts, Amherst.
- FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105:1–41.
- FULLER, T. K., AND P. R. SIEVERT. 2001. Carnivore demography and the consequences of changes in prey availability. Pp. 163–178 in *Carnivore conservation* (J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, eds.). Cambridge University Press, London, United Kingdom.
- GREEN, B., M. GRIFFITHS, AND R. M. C. LECKIE. 1983. Qualitative and quantitative changes in milk fat during lactation in the Tammar wallaby (*Macropus eugenii*). *Australian Journal of Biological Science* 36:455–461.
- HARLOW, W. M., E. S. HARRAR, AND F. M. WHITE. 1979. *Textbook of dendrology*. 6th ed. McGraw-Hill, New York.
- HATLER, D. F. 1972. Food habits of black bears in interior Alaska. *Canadian Field-Naturalist* 86:17–31.
- 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.
- HORNER, E. R. (ED.). 1996. *Massachusetts municipal profiles, 1996–97*. Information Publications, Palo Alto, California.
- IVERSON, S. J., J. E. MCDONALD, JR., AND L. K. SMITH. 2001. Changes in the diet of free-ranging black bears in years of contrasting food availability revealed through milk fatty acids. *Canadian Journal of Zoology* 79:2268–2279.
- IVERSON, S. J., AND O. T. OFTEDAL. 1992. Fatty acid composition of black bear (*Ursus americanus*) milk during and after the period of winter dormancy. *Lipids* 27:940–943.
- JENNESS, R., A. W. ERICKSON, AND J. J. CRAIGHEAD. 1972. Some comparative aspects of milk from four species of bears. *Journal of Mammalogy* 53:34–47.
- KASBOHM, J. W. 1994. Response of black bears to gypsy moth infestation in Shenandoah National Park, Virginia. Ph.D. dissertation, Virginia Polytechnic Institute and State University, Blacksburg.
- KASBOHM, J. W., M. R. VAUGHAN, AND J. G. KRAUS. 1996. Effects of gypsy moth infestation on black bear reproduction and survival. *Journal of Wildlife Management* 60:408–416.
- KNUTSON, R. M. 1979. Plants in heat. *Natural History* 88(3):42–47.
- LANDA, A., O. STRAND, J. E. SWENSON, AND T. SKOGLAND. 1997. Wolverines and their prey in southern Norway. *Canadian Journal of Zoology* 75:1292–1299.
- LECOUNT, A. L. 1987. Causes of black bear cub mortality. *International Conference on Bear Research and Management* 7:75–82.
- LINDSTROM, E. 1983. Condition and growth of red foxes (*Vulpes vulpes*) in relation to food supply. *Journal of Zoology (London)* 199:117–122.
- MCDONALD, J. E., JR. 1998. The effects of food supply and nutrition on black bear reproductive success and milk composition. Ph.D. dissertation, University of Massachusetts, Amherst.
- MCDONALD, J. E., JR. 2003. Methods for capturing free-ranging black bears, *Ursus americanus*, in difficult locations. *Canadian Field-Naturalist* 117:621–625.
- MCDONALD, J. E., JR., AND T. K. FULLER. 1994. Black bear food habits: beyond the same old scats. *International Union of Game Biologists* 21:293–298.
- MCDONALD, J. E., JR., AND T. K. FULLER. 1998. Testing assumptions in bear research: using statistical power analysis to estimate effects of den type on black bear cub survival. *Ursus* 10:405–411.
- MCDONALD, J. E., JR., AND T. K. FULLER. 2001. Prediction of litter size in American black bears. *Ursus* 12:93–102.
- MESSIER, F. 1987. Physical condition and blood physiology of wolves in relation to moose density. *Canadian Journal of Zoology* 65:91–95.
- NOYCE, K. V., AND D. L. GARSHELIS. 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. *International Conference on Bear Research and Management* 9:481–496.
- NOYCE, K. V., AND D. L. GARSHELIS. 1998. Spring weight changes in black bears in northcentral Minnesota: the negative foraging period revisited. *Ursus* 10:521–531.
- OFTEDAL, O. T., G. L. ALT, E. M. WIDDOWSON, AND M. R. JAKUBASZ. 1993. Nutrition and growth of suckling black bears (*Ursus americanus*) during their mothers' winter fast. *British Journal of Nutrition* 70:59–79.
- REIDMAN, M., AND C. L. ORTIZ. 1979. Changes in milk composition during lactation in the northern elephant seal. *Physiological Zoology* 52:240–249.

- SAMSON, C., AND J. HUOT. 1995. Reproductive biology of female black bears in relation to body mass in early winter. *Journal of Mammalogy* 76:68–77.
- TODD, A. W. 1985. Demographic and dietary comparisons of forest and farmland coyote, *Canis latrans*, populations in Alberta. *Canadian Field-Naturalist* 99:163–171.
- TODD, A. W., AND L. B. KEITH. 1983. Coyote demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management* 47:394–404.
- VAN ORSDOL, K. G., J. P. HANBY, AND J. D. BYGOTT. 1985. Ecological correlates of lion social organization. *Journal of Zoology* 206: 97–112.
- ZAR, J. H. 1996. *Biostatistical analysis*. 3rd ed. Prentice-Hall, Englewood Cliffs, New Jersey.

Submitted 21 July 2004. Accepted 19 January 2005.

Associate Editor was Floyd W. Weckerly.