

Body condition and growth dynamics of American black bears in northern Canada

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Abstract: We examined body condition and growth dynamics of wild American black bears (*Ursus americanus*) inhabiting interior regions of northern Canada, 1998–2009. Differences in body condition were unrelated to gender, but we found significant effects of age and season as well as an interaction between the two. We found a trend toward improved body condition in older bears that increased during summer and peaked in fall, with lowest values observed in spring. The von Bertalanffy growth function showed that males reached asymptotic body length 9.3% longer, and mass 29.3% heavier, than females. Our growth models indicated an association between sexual growth divergence and the onset of reproduction in females, together with more rapid and prolonged male growth. We suggest that sexual size dimorphism develops in part from constraints on female growth from high energetic costs of reproduction. In contrast, males experience no comparable energetic trade-off after reaching sexual maturity and apparently allocate available energetic resources to growth of larger body size, which benefits more competitive males in terms of increased reproductive success.

Key words: body condition index, growth function, Northwest Territories, *Ursus americanus*, von Bertalanffy

Ursus 23(1):12–20 (2012)

Body condition and growth dynamics affect reproductive success of American black bears (*Ursus americanus*; Elowe and Dodge 1989, Stringham 1990, Garshelis 1994, Noyce and Garshelis 1994, Costello et al. 2009). Females in poor condition abandon litters, and as female body size increases, litter size and natality increase while interbirth interval, and age of primiparity decrease (Elowe and Dodge 1989, Kolenosky 1990, Stringham 1990, Noyce and Garshelis 1994, Samson and Huot 1995). Similarly, larger males gain access to more females in estrus (Kovach and Powell 2003, Costello et al. 2009). Therefore, body condition and growth can be used as a proxy for reproductive fitness (Stringham 1990, Noyce and Garshelis 1994), and its measurements are both of general theoretical interest and broad practical application to ursid biology and management. The objective of this study was to describe for the first time the body condition and

growth dynamics of wild black bears inhabiting interior regions of northern Canada.

Study area

Data were collected in the Dehcho and North Slave regions of the Upper Mackenzie Basin in Northwest Territories, Canada (Fig. 1). The area is situated in the northern Interior Plains of the discontinuous permafrost zone. At Fort Simpson (61°51'47"N, 121°21'18"W), climate is cold, dry continental with wide monthly variations in temperature, and the total mean annual precipitation is 374 mm (210 mm rain and 164 mm snow). Summers are short but warm, with daytime highs averaging in the low 20°C range and overnight lows around 10°C. Winters are long and cold, with daytime highs around –20°C and lows around –30°C. Temperatures decrease and precipitation tends to increase with elevation, and some areas can remain snow-covered from mid-October to late-May. The region has numerous lakes, rivers, and

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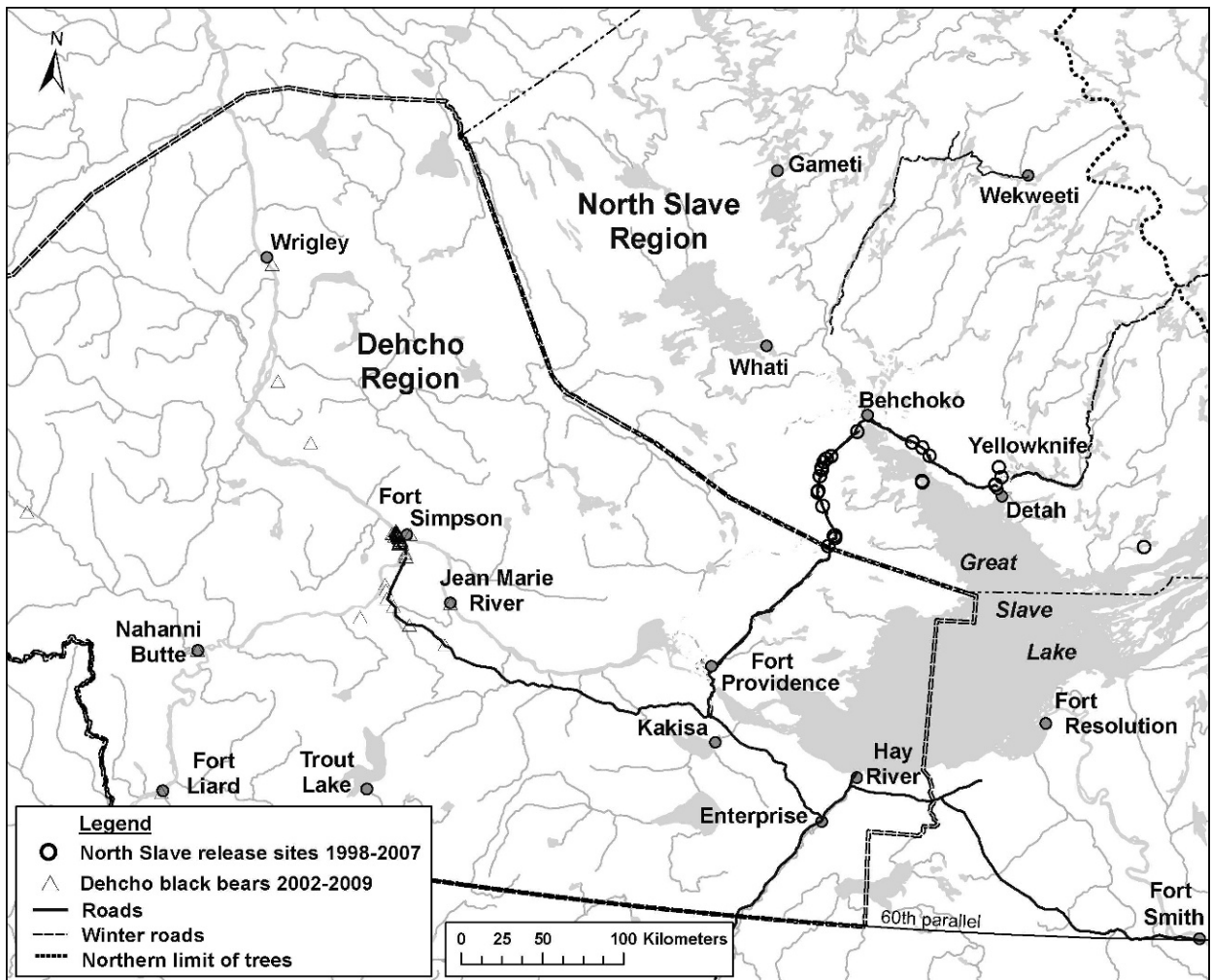


Fig. 1. Location of black bears examined in Northwest Territories (NWT), Canada, 1998–2009.

habitat features, including boreal forest in southern areas which grade into tundra with scattered trees and shrubs (Ecosystem Classification Group 2007).

In the early spring months (Apr to May), bears typically emerged from winter dens when average temperatures were rising and snow melting. During spring, bears generally moved out of the snow to feed on winter-killed animals as well as grasses, sedges, and other plants. Some bears also preyed for a few weeks during May and June on newly born boreal caribou (*Rangifer tarandus*) and moose (*Alces alces*) calves when they were vulnerable. Through the summer (Jun to Jul) and fall (Aug to Oct), they continued to eat vegetation, dig for roots and tubers, excavate insect nests, eat small mammals, and consume more available soft mast items. By fall,

diets consisted mostly of hard mast items, insect nests, and starchy tubers and roots that may be important to build fat reserves before searching for dens and for winter dormancy.

Methods

Data collection and morphometrics

Morphometric data were available for 139 bears measured by Environment and Natural Resources staff between 1998 and 2009. Most samples came from bears dispatched for public safety reasons near communities ($n = 113$) or captured and relocated ($n = 17$), with the remaining specimens coming from mortalities associated with subsistence hunters and vehicle-collisions ($n = 9$). Recorded variables for

each specimen included an identification code, date of measurement, location, straight-line body length (cm), body mass (kg), age (yr), and gender. The straight-line body length (cm) from tip of snout to base of tail was measured with a tape measure held above the bear while it was in a sternal recumbence. Contour body length (cm) was measured for 19 bears as the distance from the tip of the nose to the end of the last tail vertebra along the contour of the spine while the bear was aligned laterally. Because contour body length was not measured for all bears, we used the following modeled relationship to predict contour body length (CBL) from straight-line body length (SLBL): $CBL = 1.12 (SE = 0.01) \times SLBL$ ($r^2 = 0.998$, $P < 0.001$). Estimated CBL using this equation was on average within 0.2% of the measured SLBL, and linear regression fit had a slope of 0.92 ($SE = 0.01$, $r^2 = 0.839$, $P < 0.001$). Body mass was measured with calibrated spring scales. Age was assigned from counts of cementum annuli in an extracted first premolar tooth (Matson's Laboratory, LLC, Milltown, Montana, USA). Reproductive condition of females was not assessed.

Body condition

The body condition of each specimen was estimated using the formula developed by Cattet et al. (2002) for estimating the combined mass of fat and skeletal muscle relative to straight-line body length and mass. We constructed a 2-factor ANCOVA (type III sum of squares) to test for differences in body condition index (BCI) between genders and among seasons (spring, summer, and fall) as fixed categorical variables and age for the covariate. All potential 2-way interactions between model terms were initially included, and later removed when non-significant. We used the small-sample, bias-corrected form of Akaike Information Criterion (AIC_c) for evaluating and comparing models (Burnham and Anderson 2002). We examined model residuals to ensure validity for the appropriate model assumptions.

Growth

To compare the time of completion for development of a particular body size character between genders, we estimated age when length and mass reached 90% (t_{90}) and 97% (t_{97}) of asymptotic size. The t_{90} value was chosen for comparison between gender in the Florida black bear (Bartareau 2011) and brown bear (*Ursus arctos*; Kingsley et al. 1988, Zedrosser et al. 2006, Bartareau et al. 2011) and t_{97}

selected in polar bears (*U. maritimus*; Derocher and Wiig 2002, Derocher and Stirling 1998). We calculated t_{90} and t_{97} from the parameters of fitted von Bertalanffy (von Bertalanffy 1957) growth functions ($A(t) = A_{\infty} \times [1 - e^{-K(t-T)}]^p$), where A is body length (cm) or mass (kg) at age t (yr), A_{∞} is asymptotic body length or mass for the sampled population, K is a relative growth rate parameter or 'maturing index' that describes the rate at which an asymptote is reached (yr^{-1}), T is a fitting constant and is interpreted as the hypothetical age of an individual at zero body length or mass assuming the equation to be valid at all ages (yr), and $p = 1$ for length and $p = 3$ for mass.

Data were fitted using the Levenberg–Marquardt–Nash algorithm (Ratkowsky 1983), and the pseudo R^2 and root mean squared deviation of data points about fitted growth curve were used to evaluate the general goodness-of-fit and accuracy of model to the observed pattern of growth, respectively (Sokal and Rolf 1995). We used a t -test for independent samples to test for gender differences in asymptotic body length, mass, and maturing index estimates. Following Kingsley et al. (1988), we compared the relative development in body mass on length with a corpulence index (kg/m^3) calculated from growth model size-at-age estimates.

All tests were 2-tailed, and we considered results significant using $\alpha = 0.05$. Statistical analyses were conducted using Microsoft Excel® or Statistix® 9.0 (Analytical Software 2008).

Results

Body condition

The body condition of 39 female and 100 male bears ranged widely and overlapped (Fig. 2). The mean value for females (1.04, $SE = 0.26$), although approximately 67% greater, did not differ significantly from males (0.62, $SE = 0.17$; $F = 2.09$; 1, 130 df; $P = 0.151$), and the interaction terms gender \times age ($F = 0.56$; 1, 130 df; $P = 0.460$) and gender \times season ($F = 1.47$; 2, 130 df; $P = 0.234$) were also not significant. We found significant effects of both age ($F = 4.69$; 1, 130 df; $P = 0.032$) and season ($F = 3.89$; 2, 130 df; $P = 0.023$), with a non-significant interaction between the two ($F = 2.40$; 2, 130 df; $P = 0.094$). Slopes of the fitted lines showed that body condition estimates increased with age in spring and summer and were heterogeneous between seasons (Fig. 2). Mean body condition was lowest in spring (0.42, $SE = 0.24$, $n =$

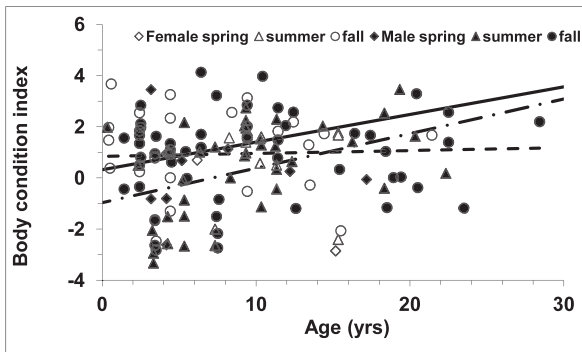


Fig. 2. Body condition index by age for female (□) and male (■) black bears in Northwest Territories, Canada, 1998–2009. Fitted lines reflect body condition estimates for fall (dashed line), spring (dashed dotted line), and summer (solid line) are heterogeneous between seasons.

11), increased during summer (0.71, SE = 0.62, $n = 49$), and peaked in fall (0.94, SE = 0.19, $n = 79$).

Growth

We fitted body length and mass-at-age measurements for specimens aged 0.3 to 28.4 years to von Bertalanffy growth functions without difficulty, and convergence criterion were met after 5 to 18 iterations (Table 1). Model fit was good for each gender and pseudo R^2 were all above 93.6%. Root mean squared deviations about the fitted length growth curves were 17.14 cm (or 10.9% of asymptote) for females and 17.59 cm (10.2%) for males. The corresponding mean squared deviations for mass growth curves was larger (19.34 kg, 21.7%) for females than males (22.17 kg, 17.6%).

Growth models for each gender showed that length and mass increased with age (Fig. 3), particularly during the early postnatal period until age

3 years, and then slowed. The t_{90} and t_{97} values for body length were 3.5 and 5.5 years, respectively for females, and 3.3 and 5.1 years, respectively, for males. Both genders grew for a greater number of years in body mass than in length; the t_{90} and t_{97} values for mass were 7.8 and 12.0 years females and 10.0 and 15.2 years for males.

Relative growth in mass on body length showed well-defined variation with age (Fig. 4). For each gender, the corpulence index was greatest soon after birth and rapidly decreased with age to minimum at about age 4 years, then increased slightly and leveled by about age 15 years. Female values started higher at 44.35 kg/m³, decreased to minimum of 20.19 kg/m³, then leveled at about 22.9 kg/m³. The corpulence index for males started slightly lower at 39.35 kg/m³, reached a minimum of 17.81 kg/m³ and leveled of at about 24.0 kg/m³.

Growth curves estimated that asymptotic length and mass were significantly larger in males than females, but we observed non-significant gender differences in maturing index values. Male asymptotic length was 9.3% longer ($t = 3.75$, 137 df, $P < 0.001$) and mass 29.3% heavier ($t = 4.38$, 137 df, $P < 0.001$) than females. Male body length maturing index was 9.5% larger ($t = 0.45$, 137 df, $P = 0.654$) and mass 20.7% smaller ($t = 0.87$, 137 df, $P = 0.388$) than females.

Discussion

Body condition and growth studies for the black bear are both of general theoretical interest and broad practical application to ursid biology and management. Our motivation for this study was to examine a population of this species inhabiting northern Canada using acquired data from routine management actions.

Table 1. von Bertalanffy growth model parameter estimates for female and male black bears in Northwest Territories, Canada. All models contain a parameter to account for asymptotic contour body length or body mass (A_{∞}), maturing index (K), and fitting constant interpreted as the hypothetical age of an individual at zero body length or mass (T). Also reported are pseudo R^2 and root mean squared deviation of data points about fitted growth curve (RMSD).

Gender	n	A_{∞} (SE)	K , yr ⁻¹ (SE)	T , yr	R^2	RMSD
Contour body length, cm						
Female	39	157.16 (3.69)	0.57 (0.12)	-0.62	0.959	17.14
Male	100	173.17 (2.27)	0.63 (0.12)	-0.47	0.981	17.59
Body mass, kg						
Female	39	89.24 (5.96)	0.29 (0.08)	-0.18	0.964	19.34
Male	100	126.30 (4.82)	0.23 (0.03)	-0.12	0.936	22.17

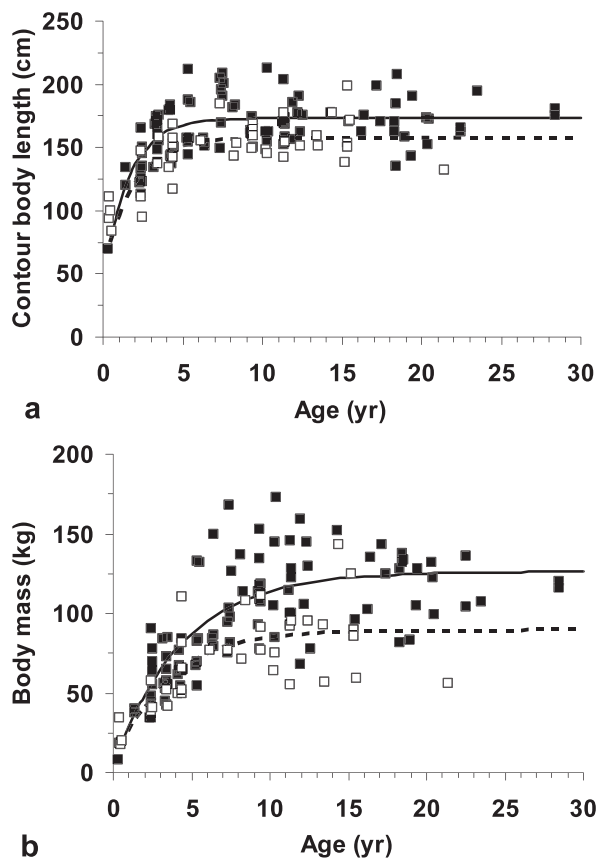


Fig. 3. Growth of female (□) and male (■) black bears in Northwest Territories, Canada, 1998–2009, as demonstrated by (a) contour body length and (b) body mass by age. Fitted lines reflect growth curve for females (dashed line) and males (solid line) as calculated from the von Bertalanffy function.

Although most of the bears sampled were categorized as nuisance bears and the samples were male dominated, we believe that the sample of bears is representative of the greater population. Our sample included bears aged 0.3 to 28.4 years, which spans the lifetime of black bears in the area. The study area was largely undeveloped (Fig. 1).

Yellowknife is situated on the shore of Great Slave Lake, and bears following the lake shore can easily pass through the community. The City of Yellowknife installed an electrified fence around the city dump in late summer 2000 that inhibited the food conditioning of wild bears.

Fort Simpson, about 360 km west of Yellowknife, is located on an island where the Liard and Mackenzie rivers meet. Bears have historically passed through the area, but now were characterized

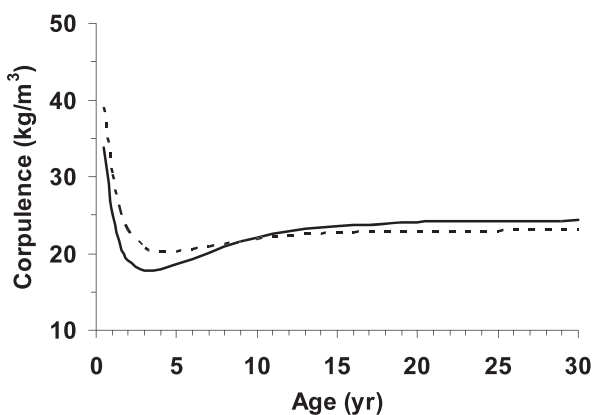


Fig. 4. Corpulence index by age for female (dashed line) and male (solid line) black bears in Northwest Territories, Canada, 1998–2009.

as nuisance bears, even though not attracted to garbage because the dump is located kilometers away from the island. The bears used for this study were not the typical food conditioned nuisance bears known from other populations in more urban-interface communities, but rather were wild bears that had wandered into town.

Body conditions of black bears varied widely, but differences were not attributable to gender. This result was not surprising because both genders are omnivorous and opportunistic feeders that consume whatever food is available (Larivière 2001); the diet of northern bears is similar to those elsewhere in Canada (MacHutchon 1989, McLellan 2011). However, age and season were important factors explaining differences in body condition, and there was a significant interaction between the two. Cattet et al. (2008) found that body condition increased with age, and the more frequently a bear was captured, the lower its age-related rate of change in body condition. This capture-related effect might occur because multiple recaptures decrease a bears' energy intake, or increase its energy use, or a combination of both (Cattet et al. 2008). Similarly, our results showed a trend toward increasing body condition with age that would not be influenced by any capture-related effect because bears were captured only once.

We found that mean body condition was highest among bears ≤ 2 years old, low in juveniles and adults aged 3–7 years, then increased and leveled off among bears ≥ 15 years old. It is not surprising that high body condition was found among the youngest

bears, coinciding with the early postnatal period of maternal care that likely reflects a mothers' nutritional benefit to her dependent offspring. An abrupt decrease in body condition coincided with the typical period from weaning through to independence, and the minimum was reached at approximately the period of family dissolution (Larivière 2001). Schroeder (1987) found that larger adults typically out-competed smaller juveniles for food, which should increase their potential for improved body condition in terms of increased mass per unit length. Under these conditions, competitive advantage is a potential explanation for some of the variation in body condition with age.

Long-term study of black bears can illustrate the close relationship between food available to them and body mass (Vaughan 2009). Although body condition may be low among independent offspring, benefits from seasonal increases or decreases in food supply should be apparent in the body condition of all ages. Our results showed that body condition, controlled for the effects of age, increased during summer and peaked in fall, with lowest values observed in spring. In British Columbia, McLellan (2011) also found that body condition varied among seasons in relation to available food, with bears caught in spring having lower values than during summer and fall. Black bears can exhaust up to 30% of mass during winter dormancy, and the rate of loss for lactating females with cubs is 45% higher than that of nonlactating bears (Nelson et al. 1973, Samson and Huot 1995, Noyce and Garshelis 1998). The mass of a bear typically increases rapidly during summer and fall in preparation for hibernation (Samson and Huot 1995, Noyce and Garshelis 1998). The increase in body condition from spring to summer and fall in this study corresponded well with the period when food supplies become more abundant and bears were increasing their food intake following winter dormancy.

Food scarcity can result in decreased body condition in general, and females inhabiting northern habitats may be more affected by food shortage than males (Jonkel and Cowan 1971), potentially lowering the quantity and quality of milk for cubs of mothers in physiological stress (Jonkel and Cowan 1971, Elowe and Dodge 1989, Kolenosky 1990, Noyce and Garshelis 1994). Females that would normally reproduce may either fail to breed or lose their young in utero or post partum due to insufficient body condition (Elowe and Dodge

1989, Noyce and Garshelis 1994). If body condition were important for female reproductive fitness, then one would expect individuals to respond to limited food availability by allocating a greater proportion of available energy to reserves at the expense of increased bodily growth. We found that females had higher average body condition values than did males, although differences were non-significant. Unfortunately, our sample did not include information on female reproductive condition; future research should determine whether there is a minimum threshold body condition below which reproduction is negatively affected.

The von Bertalanffy model accounted for $\geq 93.6\%$ of variation in body length and mass growth curves. However, the remaining variability indicates that other factors, independent of age, that were not included in the model, might also have affected the growth curves. A non-age factor such as individual variability may cause part of the observed variation in growth of bears. Geographical differences in black bear growth rates have been reported (Mahoney et al. 2001) and a variety of different habitats and food resources can be found within the area occupied by a study population (Ecosystem Classification Group 2007). In such a scenario, variation in growth rates within a bear population would be expected if individuals used areas providing different food resources.

Of the 2 body measures we modeled (Fig. 3), the estimate for body mass was much more variable than body length. The high pseudo R^2 and low root mean squared deviation of data points about the fitted growth curve for body length-at-age data is logical because length is a reliable measurement that represents inflexible skeletal growth (Eason et al. 1996). Greater variation in body-mass growth estimates were expected because of potential temporal variation in body mass measurements independent of age (Samson and Huot 1995; Noyce and Garshelis 1994, 1998; McLellan 2011). Thus, body length represented basal growth pattern better than did mass. Variation in estimates of body mass growth (17.6 and 21.7% of male and female asymptotes, respectively) was within the range that might be expected to occur normally from differences in time since last feeding, how much food was consumed, seasonal accumulation or loss of fat, or mass gain of a pregnant female in full-term. Thus, we believe that our von Bertalanffy model parameter estimates are reasonable for the observed biological data and accurately estimated the population's body length- and mass-at-age growth curves.

Our growth models showed that both genders grew most rapidly during the early postnatal period, and most of a bear's adult lifetime was spent near asymptotic size (Fig. 3). The variation in corpulence index values (Fig. 4) of bears with age suggests that, compared with older and slower-growing bears, younger and faster growing bears were expending more acquired energy relative to basal growth (i.e., body length) than to body mass. In length growth, males matured slightly earlier than females, reaching t_{90} and t_{97} 0.2–0.4 year younger. Mahoney et al. (2001) reported that both sexes of black bears in northern populations continued growth in body length until about age 9 years, which corresponds well with closure of the skull and long bones (Rausch 1961, Sauer 1975). At age 9 years, our models estimated that growth in body length of both genders was nearly complete, reaching $\geq 99.6\%$ of asymptote.

Growth models demonstrated that both genders grew in body mass for more years than in length (Fig. 3), consistent with studies of brown (Kingsley et al. 1988, Bartareau et al. 2011) and polar bears (Derocher and Stirling 1998, Derocher and Wiig 2002), as well as other populations of black bears (McRoberts et al. 1998, Mahoney et al. 2001, Bartareau 2011). The maturing index values for body mass growth of females and males were 50.9% and 36.5% smaller than those for length, respectively. The t_{97} values were reached at age 12.0 years in females and 15.2 years for males, which were similar to estimated ages at maximum size observed by Mahoney et al. (2001) of 12 years for females and 16 years for males in other northern populations.

Individual variation in length and mass growth were greater than differences due to gender among offspring through to about age 3 years. Black bear offspring typically remain with their mother for 1.5 to 2 years before weaning and becoming independent (Larivière 2001). This implies that both genders grow at the same rate during this early dependent period because more rapid growth must occur for one gender to reach a larger size than another of the same age. However, there was well-defined male-biased sexual size dimorphism by age 4. The estimated sexual size dimorphism was 16.01 cm for length (or 10.2% of female asymptote) and 37.1 kg (41.5%) for mass. Therefore, the proximate cause resulting in sex-differences in rate of growth apparently occurs after weaning.

Because female black bears invest considerable energy in lactation and rearing offspring that would

otherwise be available for growth in body size (Oftedal et al. 1993, Farley and Robbins 1995, Harlow et al. 2002), females should begin to grow more slowly in body size after reaching sexual maturity. Hence, the age at which average length growth slows and approaches asymptotic size may be used to predict when most females in a population reach sexual maturity. For instance, the leveling off of growth in length at 97% of asymptotic size suggests that females in the study population were sexually mature by age 5.5 years. This estimated age at sexual maturity is similar to that of Kolenosky (1990), who found that females in east-central Ontario reached sexual maturity at a minimum age of 4 years and most had produced their first litters by age 5 years. Female black bears in Montana also reached sexual maturity at about 5.5 years (Jonkel and Cowan 1971), but black bear populations further south reached sexual maturity up to 2 years earlier (Sauer 1975, Alt 1980, Stringham 1990, Noyce and Garshelis 1994, Bartareau 2011). Rausch (1961) suggested that the age at which females become sexually mature differs with latitude because of different growth rates. This may explain the later sexual maturity of females in Montana, Ontario, and this study population.

Whereas costs of reproduction and environmental conditions may constrain female growth, these cannot explain male-biased sexual size dimorphism. Little is known about the age at sexual maturity of male black bears (Larivière 2001), but genetics indicate that males in some populations may become sexually mature as early as 3 years old (Costello et al. 2009). As with females, early sexual maturity in males may be related to rates of growth. However, copulation is the only direct energetic expenditure for offspring by males. We found that male growth in mass did not decline as rapidly as it did for females during the likely onset of sexual maturation. This suggests that males do not experience a comparable energetic trade-off.

Males are polygynous, and their reproductive success is more variable than females because it depends on the ability to acquire territory, thwart competitors, and mate successfully with females in estrus (Kovach and Powell 2003). Intraspecific competition for mates is probably intense because low population density and long birth intervals make females in estrus rare (McLellan 1994). In such a situation, larger body size should enhance the ability of males to prevail in male–male contests for

territories and access to mates during the breeding season (Kovach and Powell 2003, Costello et al. 2009). In fact, Costello et al. (2009) showed that peaks in reproductive success occurred at approximately the same age as peaks in body size characteristics and frequency of bear-inflicted wounds, suggesting body size was important for successful mating. Our growth models revealed that males grew larger than females both before and after female sexual maturity. These results suggest that males apparently allocate available energetic resources to body growth, which benefits more competitive males in terms of increased reproductive success.

Management implications

The use of body condition and growth models may provide a basis for monitoring trends in nutrition and physiological development, which, in turn, may prove useful indicators for populations experiencing environmental stress. Specifically, a population under nutritional stress should respond by reduced body condition and growth, which could depress reproductive rates.

Acknowledgments

We thank D.G. Allaire, D.R. Allaire, K. Davidge, C. Lafferty, L. Letcher, K. Pennycook, G. Tsetso, D. Villeneuve, and North Slave Region wildlife officers for assistance in data collection. We thank R. Mulders and R. Gau for coordinating tooth aging of bears, L. Pulliam for diligence in sourcing literature, the Government of the Northwest Territories for supporting black bear research, and 2 anonymous reviewers for constructive and insightful comments on this manuscript.

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Received: 30 March 2011

Accepted: 1 December 2011

Associate Editor: G. Hilderbrand