POPULATION DENSITY AND FOOD CONDITIONS DETERMINE ADULT FEMALE BODY SIZE IN BROWN BEARS

Andreas Zedrosser, Bjørn Dahle, and Jon E. Swenson*

Department for Integrative Biology, Institute for Wildlife Biology and Game Management, University of Natural Resources and Applied Life Sciences, Peter Jordan Street 76, 1190 Vienna, Austria (AZ)
Department for Ecology and Natural Resource Management, Norwegian University of Life Sciences, Postbox 5003, 1432 Ås, Norway (AZ, JES)
Department of Biology, Program for Experimental Behavior and Population Ecology Research, University of Oslo, Postbox 1066, Blindern, 0316 Oslo, Norway (BD)
Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway (JES)

We investigated growth and determinants of adult female body size in brown bears (*Ursus arctos*) in 2 study areas in Sweden. Scandinavian female brown bears reached 90% of their asymptotic size at 4.1–4.7 years. Four factors were considered in our analysis of the determinants of adult female size: annual food conditions, population density, multilocus heterozygosity, and yearling body size. Our results suggest that individual body size variation of female brown bears is negatively related to density-dependent factors and positively correlated to density-independent fluctuations in the environment. Density-dependent factors may operate by increasing competition for food, resulting in a decrease in body size. Food resources for brown bears in Sweden fluctuate annually in the boreal forest and influence individual body size. Multilocus heterozygosity and yearling body size were not important in explaining adult size, because initially smaller individuals show compensatory growth when experiencing good food conditions.

Key words: body size, brown bear, condition, growth, heterozygosity, population density, *Ursus arctos*

Body size and growth are important life-history traits, influencing behavioral, anatomical, and physiological characteristics of an organism. Faster-growing and larger females usually reproduce earlier in life, produce more offspring, produce offspring of better quality, and avoid predation better than smaller females (Stearns 1992). Therefore, investigating growth patterns and the factors determining adult size are ecologically very relevant.

Density dependence in growth, body size, and mass has long been recognized in populations of large mammals (Fowler 1987). Population density can influence body size through a decrease in quantity or quality of food and a resulting increase in intraspecific competition (Clutton-Brock et al. 1982). This results in a decrease in body mass, as has been reported in several ungulate species (e.g., Hjeljord and Histøl 1999; LeBlanc et al. 2001; Skogland 1990). Density-dependent changes in life-history characters are thought to occur at population levels close to the carrying capacity (Fowler 1981a, 1981b).

Changing food conditions due to density-independent environmental fluctuations also have been reported to influence body size in ungulates (e.g., Solberg et al. 2004). Food availability differs among years and thus affects growth patterns of subadult individuals and ultimately their adult size. In ungulates, cohort effects on life-history parameters have been found repeatedly (e.g., Albon et al. 1987; Post et al. 1997; Skogland 1990), and size as adult is often positively correlated with body mass at birth or weaning (Albon et al. 1987; Festa-Bianchet et al. 2000). The sexes may be affected differently, because it has been shown in ungulates that females may exhibit compensatory growth, whereas males do not (e.g., Toïgo et al. 1999).

Surrogates for individual fitness have been reported to correlate with multilocus heterozygosity; however, the topic remains controversial (Britten 1996). Significant multilocus heterozygosity–fitness correlations have been found in birds (e.g., Hansson et al. 2001) and mammals (e.g., Coltman et al. 1998; Slate et al. 2000). Coltman et al. (1998) examined the relationship between fitness-related traits and microsatellite

* Correspondent: jon.swenson@umb.no

heterozygosity in wild harbor seal (*Phoca vitulina*) pups and found that birth mass was positively influenced by individual heterozygosity.

In large mammals, research on growth and its determinants has almost exclusively been carried out in ungulates (e.g., LeBlanc et al. 2001; Solberg et al. 2004; Toïgo et al. 1999), and little is known about this subject in large, terrestrial carnivores, except for some research in polar bears (*Ursus maritimus*). The understanding of population dynamics of large ungulates is limited not by the lack of models and theories, but by the availability of data on natural populations (Eberhardt 1985; Gaillard et al. 2003). This is even more relevant for large carnivores, a group of animals that is excessively difficult to study. They are often secretive, difficult to capture, and have a long life span and long intervals between reproductive events. Our 20-year study of brown bears (*Ursus arctos*) in 2 study areas in Scandinavia allows us to investigate these questions, because we have followed individuals from birth until death and taken repeated measurements of body size of marked animals as juveniles and adults.

The brown bear is a large terrestrial carnivore with a multi-year growth pattern (Schwartz et al. 2003). Brown bears exhibit large seasonal fluctuations in body mass because they store adipose tissue during summer and autumn for winter hibernation (Hilderbrand et al. 1999). Large interannual variation occurs in food availability. Therefore, body mass is an unreliable measure of body size in brown bears, and we focused our analysis only on skeletal size measured as head circumference (hereafter called body size; for further details refer to "Materials and Methods"). Dahle (2003) evaluated the effects of several factors on the body size of yearling brown bears and found that yearling body size was positively correlated with maternal size and negatively correlated with litter size. Yearling body size also showed a pronounced variation among cohorts, suggesting effects of changing food availabilities. In addition he found a significant negative relationship between yearling body size and population density (Dahle 2003).

Male reproductive success in polygynous, size-dimorphic species is dependent on body size (Andersson 1994), and males probably have been selected to maximize growth rate (Clutton-Brock et al. 1988). In contrast, females in size-dimorphic species have to trade growth for reproduction and cannot grow as fast; several studies have suggested different growth patterns between males and females in ungulates (e.g., Festa-Bianchet et al. 1994; LeBlanc et al. 2001; Toïgo et al. 1999). Brown bears exhibit a polygynous mating system and strong sexual size dimorphism (Schwartz et al. 2003). Therefore, we restrict our analysis to female brown bears only. We investigated the growth patterns of female brown bears with the Bertalanffy growth curve (Bertalanffy 1938), and investigated 4 factors that are likely to determine female adult body size: population density, food conditions, size at weaning, and multilocus heterozygosity. Specifically, we predicted that adult body size of female brown bears is negatively related to population density, is positively correlated to the food conditions experienced as a subadult, is positively correlated with yearling body size, and is positively correlated with multilocus heterozygosity.

MATERIALS AND METHODS

Study area and study populations.—The study areas were in Dalarna and Gävleborg counties in south-central Sweden (approximately 61°N, 14°E, southern study area), and in Norbotten County, northern Sweden (approximately 67°N, 18°E, northern study area). Both areas are close to the northern and southern edges of the range of the Scandinavian brown bear population and are approximately 600 km apart. The southern study area (south) consists of 13,000 km^2 of intensively managed boreal forest in a rolling landscape. The forest is dominated by Scotch pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), but deciduous trees such as mountain birch (*Betula pubsecens*), silver birch (*Betula pendula*), European aspen (*Populus tremula*), and gray alder (*Alnus incana*) are common. The elevations range from about 200 m in the southeastern part to about 1,000 m in the western part, but only a minority of the area is above timberline, which is about 750 m in elevation. The mean temperatures in January and July are −7°C and 15°C, respectively. Snow cover lasts from late October until early May and the growing season is about 150–180 days (Moen 1998). Average precipitation is approximately 600–1,000 mm annually (Lundqvist 2002). Bears are intensively hunted in the entire area.

The northern study area (north) encompasses 8,000 km^2 of mountainous national parks and adjacent forested land about 100 km north of the Arctic Circle. The area is characterized by deep valleys, glaciers, and high plateaus ranging up to 2,000 m. The valleys are dominated by mountain birch, Scotch pine, and Norway spruce. Mountain birch forms the tree line and occurs at a maximum elevation of 600 m (Grundsten 1997). The mean temperatures in January and July are −13°C and 13°C, respectively. Snow cover lasts from beginning of October until late May, and the growing season is about 110–130 days (Moen 1998). Average precipitation is approximately 500–1,000 mm annually (Påhlson 1984). Bears are protected in the national parks, but hunted in the surrounding areas.

Capture, handling, and body size measurements.—Lone female brown bears and females with yearling cubs were immobilized with a dart gun from a helicopter in mid-April in the southern study area and early May in the northern study area, shortly after den emergence. We used 2.5 mg of tiletamin hydrochloride combined with 2.5 mg of zolazepam hydrochloride (Zoletil, Virbac, Carros, France), and 0.02 mg of medetomidin hydrochloride (Domitor, Orion Pharma Animal Health, Turku, Finland) per kilogram to immobilize the bears. Atipamezol hydrochloride (Antisedan, Orion Pharma Animal Health) was used as an antidote for medetomidin (5 mg per 1 mg of medetomidin—Kreeger et al. 2002). A tissue sample was taken for genetic analysis. Body length (in cm) was measured from the tip of the nose to the caudal end of the last vertebra in the tail. Head circumference (in cm; at the widest part of the zygomatic arch between eyes and ears) was measured with a tape measure and used as a surrogate measure of overall size of a female. Head circumference was used because Derocher and Stirling (1998) suggested that head measurements rather than body length might provide the most useful measures to compare populations of polar bears. In our study we used only females of known age, which we had followed from yearling to adult age. Female brown bears can start producing litters at the age of 4 years (Schwartz et al. 2003); we therefore defined a female as an adult if it had reached at least this age. For ethical reasons we did not capture females with cubs of the year, and thus not all females were measured at the same adult age. Therefore, we corrected for age in our statistical analysis. Because all bears were captured within a 2-week period in each study area, we did not adjust body size for capture date. All capture and handling conformed to the guidelines established by the American Society of

Mammalogists (Animal Care and Use Committee 1998) and the current laws regulating the treatment of animals in Sweden and were approved by the appropriate Swedish ethical committee (Djuretiska nämden i Uppsala).

Individual population density index, northern study area.—From 1995 to 2002 virtually every adult male and female and all subadult female bears were radiomarked in the northern study area (Swenson et al. 2001). We calculated the arithmetic mean of the radiolocations of every radiocollared adult and subadult bear in 2002 (the year with most radiomarked individuals). From this mean center we calculated the distance to the arithmetic mean centers of all other radiomarked bears throughout the entire study period. We then counted the number of bears (adult males and females and subadult females) surrounding a given individual within a certain radius. We chose a radius of 17.84 km because it approximates an area of 1,000 km^2 commonly used as the basis of density measure for bears (McLellan 1994); the median adult male home range was 833 km^2 in this area (Dahle and Swenson 2003). The number of cubs present per adult female was estimated by dividing the mean litter size in our northern study area (2.4—Swenson et al. 2001) by the mean litter interval (2.6 years—Swenson et al. 2001), which resulted in an estimated 0.92 cubs present per adult female per year. Because no radiomarked subadult males were represented in the initial count of bears surrounding a given individual, we multiplied the number of subadult females by 2, assuming an even sex ratio (Bellemain et al. 2005). The individual density index (I_d) in a radius of 17.84 km was calculated as $I_d = N_{ad.m} + 1.92N_{ad.f} + 2N_{subad.f}$, where $N_{ad.m}$ is the number of radiomarked adult males, $N_{ad.f}$ is the number of radiomarked adult females, and $N_{subad.f}$ is the number of radiomarked subadult females. Using the software ArcView GIS 3.2a (Environmental Systems Research Institute, Inc., Redlands, California) we subtracted the area within the 17.84-km radius around a bear that extended beyond the borders of our study area, and extrapolated the number of bears to an area of 1,000 km^2.

The Scandinavian brown bear population has expanded in size and distribution (Swenson et al. 1995). Sæther et al. (1998) reported a population growth rate of 14% annually in the northern study area in the period 1985–1994. The numbers of marked animals remained similar throughout the time period 1995–2002, despite a high and comparable capture effort in all years, suggesting stable densities. The temporally corrected individual density index (tI_d) for an individual bear in year y (for y < 1995) was then $tI_d = I_d/1.14^{(1995−y)}$, where I_d is the individual density index for 1995–2002. The estimates of individual population density indices in both our study areas rely on the assumption that the spatial distribution obtained in 2002 (northern study area) and 2001–2002 (southern study area, see below) reflect the spatial distribution in both study areas over the entire study period.

Individual population density index, southern study area.—A population size estimate, based on a DNA analysis of noninvasive sampling of scats, was carried out in the southern study area in 2001 and 2002 (Bellemain et al. 2005). We have used these results as a basis to calculate an individual density index around each individual in our analysis. For each radiocollared bear, we counted the number of genetically identified individuals within a 17.84-km radius, based on the centers of the locations of all scat samples for each individual. Also here we chose a radius of 17.84 km; the median adult male home range was 1,055 km^2 in this area (Dahle and Swenson 2003). Bellemain et al. (2005) found that 71% of all radiocollared bears in the southern study area were represented in the genetic sample. To account for the individuals not detected in the noninvasive population sampling, we divided the individual density index by 0.71. The resulting individual density index (I_d) thus can be expressed as $I_d = N_i/0.71$, where N_i is the number of genetically identified individuals surrounding a radio-

collared bear. We subtracted the area within the 17.84-km radius around a bear that extended beyond the borders of our study area using global information system maps, and extrapolated the number of bears to an area of 1,000 km^2.

Sæther et al. (1998) estimated a population growth rate of about 16% annually in our southern study area for the period 1985–1995. Population size and density estimates based on aerial capture–mark–recapture techniques were carried out in the southern study area in 1993 (Swenson et al. 1995) and again in 2001 (Solberg and Drageset 2003). Both estimates yielded very similar results, suggesting that although the population in the general area had increased in size and range, densities in the intensive study area had stayed about the same in the period 1993–2001. To temporally correct the individual population density indices for this period, we assumed stable densities from 1993 to 2002. The temporally corrected individual population density index (tI_d) for an individual bear in year y (for y < 1993) was then $tI_d = I_d/1.16^{(1993−y)}$, where I_d is the index for 2001–2002. We are confident that these individual density indices are comparable between the northern and southern study areas, because actual densities were estimated in both areas with high (~71%, south) to very high (~100%, north) proportions of marked animals in both cases.

Environmental condition index.—We used spring body mass of yearlings in a given year and study area as the basis to construct an index of the general food condition of the study populations for each year. Spring body mass (i.e., body mass after hibernation) in brown bears is dependent upon the previous year's environmental conditions because of interannual variations in food availability. Skeletal size measurements cannot be used for these purposes because they do not show the same interannual fluctuations as body mass. Yearling body mass is used as basis for this index, because body mass of 1-year-old individuals is not influenced by growth and mass gain during years other than the previous, and thus reflects the food availability of this previous year. Rather than using the actual values and just controlling for sex (Garshelis 1994; Swenson et al. 2001), we regressed yearling body mass as a function of maternal size, litter size, sex, and individual population density. In this way we controlled for variables that are known to influence yearling mass independently of environmental conditions (Dahle 2003). The standardized residuals from this regression were sorted by study area and year and the average value for each year and area was then used as the food condition index for the year before the yearlings were weighed. Taylor (1994) has defined "subadult" to refer to a weaned bear during the years required to reach reproductive maturity. To estimate the effect on adult body size of the individually experienced food conditions throughout the subadult period, we averaged the indices from age 1 to the age at which an individual female was 1st measured as an adult.

Multilocus heterozygosity.—Eighteen microsatellite primers, described in Patkeau and Strobeck (1994) and Taberlet et al. (1997), were amplified using polymerase chain reaction. The amplification and analysis of microsatellites was carried out following the protocol described in Waits et al. (2000). Individual multilocus heterozygosity was then calculated as the number of heterozygous loci divided by the number of typed loci per individual.

Statistical data analysis.—The Bertalanffy curve was used for growth curve analysis, because it has been used previously to describe the growth of bears (Derocher and Stirling 1998; Derocher and Wiig 2002; Kingsley et al. 1988). The Bertalanffy size-at-age equation was used in the form

$$s_a = S(1 − e^{−k(a−A)})^3$$

where s_a is head circumference (in cm) at age a, S is asymptotic head circumference (in cm), k is a size growth rate constant (year$^{−1}$), and A

TABLE 1.—Parameter estimates for the Bertalanffy size-at-age curves for head circumference of female Scandinavian brown bears ($\pm SE$). S is the asymptotic head circumference, k is the size growth constant, and A is the theoretical age at which the animal would have size 0.

Study area	S (cm)	k (year^{-1})	A (years)	n
North	61.50 ± 0.69	0.368 ± 0.038	−4.01 ± 0.49	68
South	62.62 ± 0.49	0.445 ± 0.034	−3.47 ± 0.33	115

is a fitting constant (extrapolated age at zero size; in years). Several individuals were captured more than once during our study period; we used only the measurement taken at the greatest age in our analysis.

In addition to the potential determinants of adult size in female brown bears presented in the introduction, we controlled for the effect of study area. The study areas were 600 km apart and bears in the north inhabited a less-productive and mountainous area and occurred at generally lower overall population densities. Therefore, we also included interactions with the study area into the statistical analyses. We also included nonlinear effects of population density in the analyses. Bears grow throughout several years of their life (Kingsley et al. 1988); therefore, we also controlled for the effect of age on adult body size. The result of the von Bertalanffy curves was used to evaluate whether a nonlinear effect of age should be included in the analysis.

We used general linear models and tested several candidate models with 1 or more explanatory variables and interaction between the variables, based on knowledge about bear biology, while controlling for the effects of study area and age. To select the most appropriate model from a set of candidate models based on the predicted relationships, we used Akaike's information criterion (Burnham and Anderson 2002), corrected for small sample sizes (AICc), which is based on the principle of parsimony. The model with the lowest AICc is considered to be the one explaining most of the variation by using the fewest parameters, but models with ΔAICc < 2 should receive consideration in making inferences (Burnham and Anderson 2002). The statistical package R 1.9.0 (R Development Core Team; http://www.R-project.org) was used in all statistical analyses.

RESULTS

Head circumference was used as a surrogate measure for overall size rather than body length, because head measurements may provide the most useful measures to compare populations in bears (Derocher and Stirling 1998) and it showed a lower coefficient of variation ($CV = 0.174$) than body length ($CV = 0.185$; $n = 525$, including recaptures). Both measures were highly correlated ($r = 0.944$, $P < 0.001$, $n = 525$), so a direct comparison with data published elsewhere is warranted.

The Bertalanffy curve was successfully fitted to head circumference data for females in both study areas, 68 in the north and 115 in the south (Table 1; Fig. 1). The growth curves were significantly different ($F = 6.3$, $P < 0.001$, $n = 183$). Female brown bears in the south grew faster (Table 1; Fig. 1) and reached 90% of their asymptotic head circumference at 4.1 years of age, whereas those in the north reached 90% asymptotic head circumference at 4.7 years.
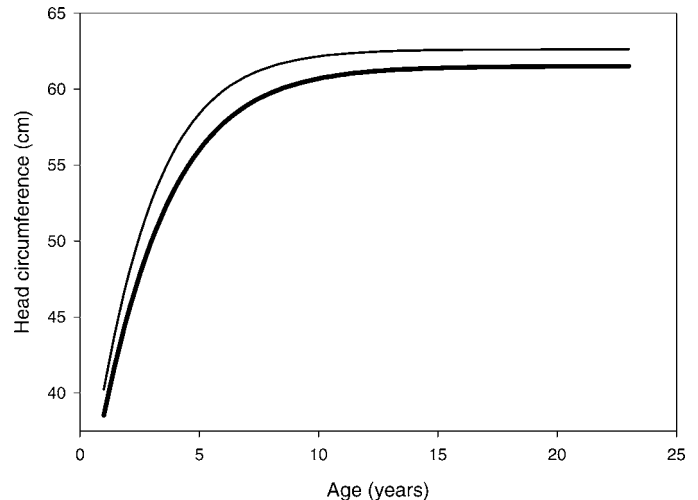

FIG. 1.—The Bertalanffy curve fitted to age and head circumference of female Scandinavian brown bears. The thick solid line represents females in the northern study area and the thin solid line, females in the southern study area.

We obtained body size measurements of 43 individual females as yearlings and as adults (20 in the north, 23 in the south). Adult head circumference varied from 49 to 63 cm ($\bar{X} = 57.3$ cm ± 3.2 SE). Nine individuals were measured at 4 years, 17 at 5 years, 15 at 6 years, and 2 at 7 years. Because 39 (91%) of the individuals used in the analysis had already reached the threshold of 90% of their asymptotic head circumference, we used age as a nonlinear variable. A model with age as the only explanatory variable explained 27.9% of the variation in adult female size ($\beta = 2.204$, $t = 3.89$, $P < 0.001$).

Four models explaining adult female size in brown bears were selected based on their AICc values, while controlling for the effect of age (Table 2). Bears were larger in the south and older bears were larger than younger bears (models 1–4). As predicted, adult female size was positively related to food conditions (models 2 and 3) and negatively related to population density (models 1, 2, and 4). Two interaction terms were considered important by our model selection procedure. The interaction study area × population density suggested that the effect of population density was stronger in the south than in the north (model 1). The interaction study area × food condition index suggested that there was less effect of food conditions on adult female size in the south (models 2 and 3). All models including an interaction population density × food condition index, or the variables yearling body size or genetic heterozygosity or both and corresponding interactions were ranked with ΔAICc > 2 and were thus not considered to be significant in explaining adult female size in brown bears (models not shown). Models using age as factor variable to control for different effects per age and corresponding interactions were not selected by the AICc.

DISCUSSION

Much (about 50%) of the individual variability in body size was explained by age, as expected because the species shows a

TABLE 2.—Parameter estimates and test statistics for the general linear model explaining adult size in female Scandinavian brown bears. Corrected Akaike information criterion (AICc) shows the corresponding value of the entire model and ΔAICc denotes the differences in AICc values. Only models with AICc $\leq$ 2 are shown. $n = 43$ (20 in the northern study area and 23 in the southern study area).

Explanatory variables	d.f.	β	SE	t	P	R^2	AICc	ΔAICc
Model 1						0.53	191.93	0.00
Study area	1							
North		0	0					
South		4.415	1.007	4.382	0.000			
Age	1	2.128	0.481	4.421	0.000			
Population density index	1	−2.741	0.983	−2.788	0.008			
Study area × population density index	1							
North		0	0					
South		2.174	1.132	1.919	0.063			
Model 2						0.56	192.32	0.39
Study area	1							
North		0	0					
South		3.175	1.046	3.035	0.004			
Age	1	2.067	0.502	4.119	0.000			
Population density index	1	−0.801	0.510	−1.569	0.126			
Environmental condition index	1	1.047	0.489	2.141	0.039			
Study area × environmental condition index	1							
North		0	0					
South		−1.646	0.826	−1.993	0.054			
Model 3						0.53	192.50	0.57
Study area	1							
North		0	0					
South		2.051	0.778	2.637	0.012			
Age	1	2.000	0.510	3.922	0.000			
Environmental condition index	1	1.301	0.470	2.766	0.009			
Study area × environmental condition index	1							
North		0	0					
South		−1.727	0.841	−2.054	0.047			
Model 4						0.48	193.47	1.54
Study area	1							
North		0	0					
South		3.675	0.964	3.812	0.000			
Age	1	2.256	0.494	4.570	0.000			
Population density index	1	−1.098	0.501	−2.193	0.035			

multiyear growth pattern (Schwartz et al. 2003). However, once this effect was accounted for, we found significant positive effects of food conditions and negative effects of population density on adult size in female brown bears. We also found significant differences between the study areas. Females were larger and grew faster in the south. In addition, we found significant interactions between study area and population density and study area and environmental conditions. In contrast to several studies of ungulates, we did not find a relationship between size when young and as an adult; that is, females seemed to be able to compensate for size disadvantages at weaning. We also found no correlation between multilocus heterozygosity and adult size.

As predicted, we found a negative influence of population density on adult female size in brown bears. Density-dependent relationships for body size and body mass have been reported in several studies of large mammals, especially ungulates (e.g., Festa-Bianchet et al. 2000; Hjeljord and Histøl 1999; Skogland 1990). In general, an increase in population density increases competition for food, often resulting in a decrease in body size and mass. In contrast to ungulates, the evidence from density-dependent size and growth effects in large carnivores is comparatively scarce. Fowler (1990) found that density-dependent changes in the northern fur seal (*Callorhinus ursinus*) included aspects of growth. Increasing population density has been reported to affect yearling weights in American black bears (*Ursus americanus*—Garshelis 1994), body length of juvenile polar bears (Derocher and Stirling 1998), and possibly adult body size in another polar bear population (Derocher and Wiig 2002).

Overall population density appears to be related to food availability in bears (McLellan 1994), suggesting that food is the ultimate regulating factor. Density dependency may work by reducing the food base, increasing competition for food, or both. In systems where food is highly concentrated and renewed quickly (e.g., salmon [*Oncorhynchus*] rivers), foraging efficiency is likely impaired by social behavior at high densities (McLellan 1994). However, in systems where food is more evenly distributed (e.g., berries), food depletion at high population densities may be more significant (Welch et al. 1997). The populations in this study did not seem to experience severe food constraints, because they showed a high population growth rate during 1984–1995 (Sæther et al. 1998). But, on the other hand, the overall density in the south had not changed notably over the last 10 years (Solberg and Drageset 2003), suggesting that the population was near or approaching carrying capacity or was held at that level by hunting. We found that the effect of density was stronger in the south than in the north, perhaps because the density was higher in the south ($\sim$30 bears/1,000 km^2) than in the north ($\sim$11 bears/1,000 km^2). Most likely because of more severe environmental conditions, carrying capacity may be lower in the north, which also was suggested by the interactions indicating that annual food abundance had a greater impact on adult size in the north. Our results support the physiological constraint hypothesis: adult female bears were smaller at high densities because their growth was limited by resource availability.

As predicted, we found positive effects of environmental conditions bears experienced while a subadult on adult female body size. Available nutrition is probably the most important factor affecting growth (Laws 1956). Several studies have investigated the impact of density-independent environmental fluctuations on body size in large mammals, mostly ungulates. However, most of them dealt with cohort effects, that is, conditions experienced during the year of birth. Cohort effects lasting to adulthood have been found in several life-history traits among different ungulates (Gaillard et al. 2003 [for a review in deer]; Solberg et al. 2004; Toïgo et al. 1999). Lack of compensatory growth appears to be the rule rather than the exception, although most of these studies have been carried out in populations with high or highly variable density (Solberg et al. 2004).

Dahle (2003) has shown a significant cohort effect on yearling size in brown bears. Our results suggest these effects do not persist throughout life for female brown bears, because, contrary to our prediction, yearling body size was not important in explaining adult size. The relevant candidate model with the effect of yearling size on adult female size was neither significant nor did it show any trend (β of yearling size = 0.002, P = 0.988), when controlling for study area and age. Atkinson et al. (1996) examined the relationship between growth early in life and adult body size in polar bears. They found that adult body length was significantly correlated with length in 2-year-old females (Atkinson et al. 1996). However, we did not find a relationship between female yearling size and adult female size in brown bears. These differences in two closely related ursid species may be related to environmental and food conditions. The polar bear lives in a highly variable arctic environment and feeds primarily on ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*), which are unevenly distributed both temporally and spatially (Atkinson et al. 1996). Hunting efficiency of subadult females may be less than that of adults (Stirling and Latour 1978). Scandinavian brown bears feed mainly on moose (*Alces alces*) and ants (*Formica* and *Camponotus*) in spring and berries (*Vaccinium* and *Empetrum hermaphroditum*) during summer and autumn (Dahle et al. 1998). Especially the distribution and abundance of berries can vary in both time and space (Kardell and Eriksson 1990), however, most likely not to the extent as for seals. In addition, Nilsen (2002) has shown that Scandinavian bears can compensate for crop failure of one berry species by eating more of other berry species and no specialized hunting skills are necessary. This may enable subadult female brown bears to show compensatory growth, whereas subadult female polar bears are not able to compensate for initially small body size.

A female bear may promote compensatory growth by delaying sexual maturity, to become more efficient at foraging and attain a larger body size (Taylor 1994), a pattern also observed in ungulates (e.g., Green and Rothstein 1991). Støen et al. (2006) showed that approximately 40% of Scandinavian female brown bears disperse from their natal range. Therefore, another possibility for small subadult females to achieve compensatory growth would be to disperse into lower-density areas.

We found that the effect of environmental conditions on growth and adult size in female brown bears was stronger in the north than in the south and that northern adults were smaller and grew more slowly. Kojola and Laitala (2001) investigated variations in body size of brown bears throughout Finland and found that male brown bears were larger in the south; however, they were not able to document the same for females. McNab (1971) did not find statistically significant associations between latitude and skull measurements of brown bears in North America. Primary productivity and average temperatures that favor plant growth are higher in southern than in northern Scandinavia (Moen 1998), but forage quality may be better in climatically harsher environments (Albon and Langvatn 1992). In ungulates, nutritional quality can outweigh the effects of plant biomass on body mass (Langvatn and Albon 1986), but brown bears do not rely on browse as do ungulates. In spring Scandinavian brown bears rely mostly on protein sources (moose and ants). Their capability to obtain enough nutrition for growth and to store adipose fat tissue for hibernation relies to a large extent on the quality and abundance of berries during summer and autumn (Dahle et al. 1998), a food resource that varies in both time and space because of environmental conditions (Kardell and Eriksson 1990). Similarly, it has been suggested for polar bears that long-term climatic variation could affect growth patterns by altering availability or abundance of food (Derocher and Stirling 1998). The smaller body size of female brown bears in the north is most likely explained by the shorter growing season and the lower primary productivity there. In addition, northern females hibernate for 6.9–7.9 months, depending on their reproductive status,

whereas in the south females hibernate for 5.3–6.9 months (Manchi and Swenson 2005). Thus, southern females may be able to invest more energy into growth than in the fat accumulation necessary for hibernation.

Contrary to our predictions, multilocus heterozygosity had no influence on body size of adult female brown bears. In mammals, studies of red deer (*Cervus elaphus*—Slate and Pemberton 2002), harbor seals (Coltman et al. 1998), and black-tailed prairie dogs (*Cynomys ludovicianus*—Foltz et al. 1988) have shown a positive relationship between multilocus heterozygosity and juvenile mass. But Curik et al. (2003) found no large overall effects of microsatellite heterozygosity on morphological traits in adult horses (*Equus caballus*). The relationship between multilocus heterozygosity and individual fitness remains a controversial topic (Britten 1996), and its absence of influence on individual performance is often found because multilocus heterozygosity is only weakly correlated with inbreeding coefficient (Slate et al. 2004).

We conclude that individual variation in the body size of female brown bears is mostly related to density-independent fluctuations in the environment and density-dependent factors. Density-dependent factors may operate by increasing competition for food, resulting in a decrease in body size. The berry crop, the staple food resource of brown bears in Sweden, fluctuates because of environmental conditions in the boreal forest, thus influencing individual body size of bears. Smaller females may show compensatory growth by either delaying reproduction or possibly by dispersing into low-density areas.

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