POPULATION ECOLOGY

Brown bear body mass and growth in northern and southern Europe

Jon E. Swenson · Miha Adamič · Djuro Huber · Sigbjørn Stokke

Abstract We tested six hypotheses to explain expected geographical differences in body masses of 1,771 brown bears (*Ursus arctos*) from northern and southern Europe (Sweden and Norway compared with Slovenia and Croatia): Bergmann's rule, the fasting endurance hypothesis, and the dietary meat hypothesis, which predicted larger bears in the north; and hypotheses stressing the role of high primary productivity, high population density, low seasonality, and length of the growing season, which predicted larger bears in the south. Although brown bear populations in North America vary greatly in body mass, we found no significant difference in body mass between the two European populations using a new analytical approach incorporating modeled age-standardized body masses in linear models, when correcting for sex and season. The greater variation in North America may be due primarily to the presence of large bears that feed on salmon (*Oncorhynchus* spp.), which does not occur in Europe. Asymptotic body masses were 115 ± 9 (SE) kg in spring and 141 ± 9 kg in autumn for southern females, 248 ± 25 and 243 ± 24 kg for southern males, 96 ± 2 and 158 ± 4 kg for northern females, and 201 ± 4 and 273 ± 6 kg for northern males, respectively. Northern bears gained more body mass before hibernation and lost more during hibernation than southern bears, probably because hibernation was twice as long in the north. Northern bears gained and southern bears lost mass during the spring, perhaps due to the greater availability and use of protein-rich food in spring in the north. As reproductive success in bears is correlated with adult female body mass in interpopulation comparisons, brown bears may have relatively similar reproductive rates throughout Europe, although minimum age at primiparity and litter interval are lower in the south.

Communicated by Jean-Michel Gaillard.

J. E. Swenson (✉)
Department of Ecology and Natural Resource
Management, Norwegian University of Life Sciences,
Box 5003, 1432 Ås, Norway
e-mail: jon.swenson@umb.no

J. E. Swenson · S. Stokke
Norwegian Institute for Nature Research,
Tungasletta 2, 7485 Trondheim, Norway
e-mail: sigbjorn.stokke@nina.no

M. Adamič
Department of Forestry, Biotechnical Faculty,
University of Ljubljana, Vecna pot 83,
1000 Ljubljana, Slovenia
e-mail: miha.adamic@bf.uni-lj.si

D. Huber
Biology Department, Veterinary Faculty, University of Zagreb,
Heinzelova 55, 10000 Zagreb, Croatia
e-mail: huber@vef.hr

Keywords Body growth · *Ursus arctos* · Europe

Introduction

Body size influences most behavioral, anatomical, physical, physiological, and life-history traits of an organism (Clutton-Brock et al. 1982; Peters 1983; Stearns and Koella 1986; McNab 1989; Stearns 1992). Growth patterns are also an important component in reproduction, as attainment of approximately 80–92% of threshold mass or length has been

associated with onset of reproductive maturity in mammals in general (Laws 1956; Sadleir 1969), including brown bears (*Ursus arctos*) (Kingsley et al. 1988). The size of female bears has important implications for individuals and populations, as it has been positively related to factors such as litter size, interbirth interval, and the size and survival of the young in studies comparing both populations and individuals within a population (Rogers 1976; Blanchard 1987; Stringham 1990a, 1990b; Schwartz and Franzmann 1991; Derocher and Stirling 1994, 1996, 1998; Atkinson and Ramsay 1995; Samson and Huot 1995; Hilderbrand et al. 1999a). Several studies of bears have documented geographical differences in size (Derocher and Stirling 1998; Hilderbrand et al. 1999a; Ferguson and McLoughlin 2000; Kojola and Laitala 2001; Derocher and Wiig 2002).

Several hypotheses have been formed to explain geographical variations in size, and many have been tested using data from bears. The classic hypothesis is Bergmann's (1847) ''rule,'' which states that homeothermic vertebrates are larger in cool than warm climates (Mayr 1956). Seasonality has also been proposed as the primary agent of selection for large body size, due to increasing accumulation of body reserves in harsher environments to increase fasting endurance during periods of food shortage. This has been called the ''fasting endurance hypothesis'' (Boyce 1978; Lindstedt and Boyce 1984).

Other hypotheses suggest that size should be positively correlated with primary productivity (Rozenweig 1968), and, similarly, that female brown bears should be larger in areas with high population density, high primary productivity, and low seasonality (Ferguson and McLoughlin 2000), although Hilderbrand et al. (1999a) analyzed the amount of meat in the diet in almost the same populations of brown bears as Ferguson and McLoughlin (2000) and found that female body size correlated well with the proportion of meat in the diet. Kojola and Laitala (2001) found that the rate of growth among male, but not female, brown bears in Finland was positively correlated with the length of the growing season. Others have found little or no relationships between sizes of bears over large geographical areas (McNab 1971; Kingsley et al. 1988), or that many populations were similar in size, but some groups differed from others (Derocher and Stirling 1998; Ferguson and McLoughlin 2000).

Except for Kojola and Laitala (2001), all of these studies have been conducted in North America. Also, these studies have often used a combination of spring and autumn body masses as a basis for comparison (see Stringham 1990a, 1990b; McLellan 1994; Hilderbrand et al. 1999a; Ferguson and McLoughlin 2000). Body masses in these two seasons are usually different, with bears having higher body mass and fat mass in autumn before winter hibernation (Hilderbrand et al. 2000).

Here, we describe the body mass in two brown bear populations near the northern (Scandinavia; Sweden and Norway) and southern (northern Dinara Mountains; Slovenia and Croatia) parts of the species' distribution in Europe, referred to here as ''north'' and ''south,'' respectively. We test the hypotheses mentioned above and compare the range of body growth observed in Europe with that found in North America. Some of the hypotheses predict larger bears in northern Europe: Bergmann's rule, the fasting endurance hypothesis, and the dietary meat hypothesis. The latter predicts larger bears in the north, because a review of European studies showed that northern brown bears had a considerably higher proportion of meat in their diet than southern bears (Elgmork and Kaasa 1992). This is also the case in our study areas, with generally higher proportions of protein-rich foods (meat and insects) in the diet in the north, especially in spring (Table 1). The fasting endurance

Table 1 Occurrence of protein-rich foods in the diet of brown bears in southern Europe (Dinara Mountains) and northern Europe (Scandinavia), based on fecal volume of collected scats

Area	Meat (%)			Insects (%)			Reference
	Spring	Summer	Fall	Spring	Summer	Fall	
South							
Ljubljanski Vrh, Sl[a]	6.9	13.4	1.4	1.8	25.8	6.5	Große (1999)
Sneznik, Sl	9.1	0	2.0	1.2	20.5	12.7	Große (1999)
Plitvice Lake NP, C[b]	0	0	1	1	3	1	Cicnjak et al. (1987)
North							
Pasvik, N	52.3	38.9	14.3	2.4	6.2	5.0	Persson et al. (2001)
Jämtland, Sw	37	5	1	7	10	3	Dahle et al. (1998)
Dalarna, Sw	25	15	2	12	16	6	Opseth (1998)

The sites are listed from north to south within each region (C = Croatia, Sl = Slovenia, N = Norway, Sw = Sweden)

[a] In addition, winter scats contained 63.2% meat and no insects

[b] In addition, winter scats contained 1% meat and no insects; NP stands for National Park

hypothesis predicts larger body size in the north in both spring and autumn, because large physical size allows for the storage of more fat (Lindstedt and Boyce 1984). Conversely, the hypotheses stressing the role of high primary productivity, high population density, and low seasonality predict that bears will be larger in the south. Brown bears in the south occur in higher densities and have much smaller home range sizes than those in the north (Huber and Roth, 1993; Dahle and Swenson 2003). Although our primary goal was to test these hypotheses, the analysis also allowed us to examine differences in body mass dynamics between brown bears in southern and northern Europe.

Methods and study areas

Hunters and researchers in the south weighed the bears before they were eviscerated or skinned. The brown bear hunting season is from 1 October to the end of February in Slovenia and 1 October to 31 April in Croatia. In both countries, hunting is allowed only from elevated stands over exposed baits during moonlit nights; hunters feed carrion and corn to the bears year-round at the bait stations, with the most intensive feeding occurring during the hunting season (Huber and Frković 1993; Simonič 1994). In addition, body masses were obtained from bears killed as depredators or in traffic (Adamič 1997) and those captured for radio telemetry studies. In Sweden, hunters are required to report all kills, provide the authorities with a premolar tooth for age determination, and report body mass obtained using scales at slaughterhouses. In a few cases hunters provided the masses of field-dressed bears or bears with the skin, head, feet, and internal organs removed, rather than the whole body mass. In these cases, we estimated whole body mass from the field-dressed or slaughter masses, using published regressions (Swenson et al. 1995). Brown bears are hunted only in the autumn in Sweden, with hunting seasons from 21 August to 15 October (central Sweden) and 21 August to 30 September (northern Sweden). Hunting over baits was allowed during most of this study, and 24% of the bears shot during 1981–1998 were shot over bait (Fujita 2000). Brown bears are not hunted in Norway, but we obtained the body mass of bears killed as marauders. Spring body masses of bears captured by immobilizing them from a helicopter, usually in May, were obtained using spring scales in two study areas, one in the northern Sweden, and one in central Sweden—southeastern Norway (Swenson et al. 1994). Age estimation was determined by Matson's Laboratory (Milltown, MT, USA) based on the cementum annuli in the premolar tooth root (Matson et al. 1993). Data were obtained from Croatia during 1981–2000, from Slovenia during 1991–2001, and from Scandinavia during 1981–2003.

Because the bears were weighed over extended periods, we regressed the mass of each individual on the time of weighing. This was done separately for each sex, population, and season. Cubic regressions gave the best fit, based on R^2 values. We used these regressions to correct each body mass to a standard date for spring and autumn for constructing the growth curves. Bears in Dinara and Scandinavia differ in hibernation behavior, so body masses were corrected to a biologically meaningful date that could be compared between the populations. We chose the mean dates of den entrance and emergence for females in each population. In the north, this was 19 October in autumn ($N = 195$ dennings by 40 females) and 30 April in spring ($N = 198$ emergences by 73 females) (Friebe et al. 2001; Manchi and Swenson 2005). In the south, it was 7 December ($N = 9$ dennings by 9 females) and 21 March ($N = 9$ emergences by 9 females), respectively (P. Kaczensky and D. Huber, unpubl. data). We fitted the seasonally corrected body masses to the von Bertalanffy equation, because it has been used previously to describe the growth of bears (Kingsley et al. 1988; Derocher and Stirling 1998; Derocher and Wiig 2002; but see Mahoney et al. 2001). We used the following growth curve form (von Bertalanffy 1938; Kingsley et al. 1988):

$$w(a) = W[1 - e^{(-k_w(a-A_w))}]^3,$$

where $w(a)$ is the body mass (kg) at age a (years), W the asymptotic body mass (kg), k_w the growth rate constant (year^{-1}) and A_w a fitting constant (extrapolated age (years) at zero size). We fitted the growth curves by using iterative estimation algorithms in the SPSS nonlinear regression procedure (SPSS 2004).

Age is an important factor in analyses involving body mass as the response variable. However, it is not straightforward to apply age as a covariate in linear models, due to the strong nonlinear relationship between age and body mass. To mitigate this problem we suggest an alternative approach. Basically, we model the effect of age on body mass at an individual level to enable the generation of expected body masses at a common age for the whole population (i.e., age-standardized body masses, see Appendix 1 in the ''Electronic supplementary material''). By correcting body masses to a standard age at an individual level, we can omit age in a subsequent analysis because age is already indirectly implemented into the analysis, due to the modeling. The advantage is an improvement in the rigidity of the model because the nonlinear relationship between age and mass is avoided.

As a first step we used the von Bertalanffy growth curve to describe the general growth patterns for the populations (based on one mass per age record per bear). Then we extracted the residuals (the differences between

observed and estimated masses) and modeled them in relation to age. This relationship was then used as a correction factor in a model describing the scaled body mass discrepancy (from the von Bertalanffy growth curve) for individual bears. By using this approach we can generate individual growth curves based on one mass per age record per bear (see Fig. 1 and Appendix 1 in the ''Electronic supplementary material''). Our approach allows the expected body mass to be compared between all individuals at a common age in a linear model, while ''conserving'' individual differences in body mass. Notably, the effect of age is not removed from the analysis as it might at first seem to be; it is implicatively incorporated as a covariate in our model approach. We argue that this method is superior to using age and/or age[2] and/or age[3] directly in a linear model, because a linear, quadratic or cubic relationship linking age and body weight is an inferior descriptor for body mass development compared to the acknowledged von Bertalanffy growth pattern we used to model this relationship (before applying the analysis). We used seven years as the common age to generate body masses for the analysis. The von Bertalanffy growth curves are more reliable for young bears when older age classes are lacking. This applies in particular to adult males in the south, where the growth curves apparently do not yield a reliable asymptotic value. Thus, we considered seven years to be within the range for reliable modeling.
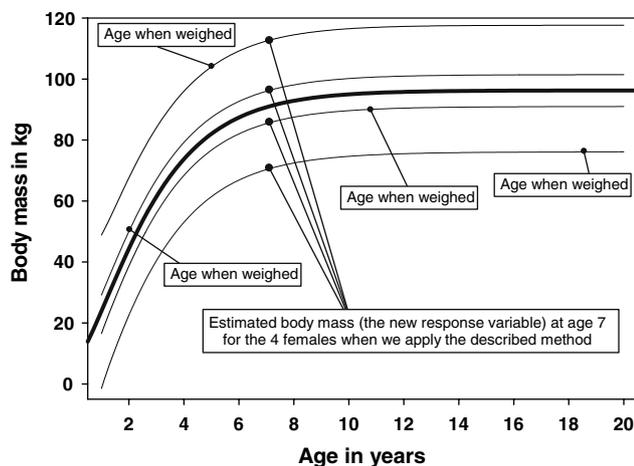

Fig. 1 The basic idea behind our approach to incorporate age indirectly as a covariate in a linear model analysis by standardizing body masses to seven years of age. The *bold curve* in the graph shows the general growth development for females in Scandinavia during spring as modeled by the von Bertalanffy equation (the same curve as in Fig. 3). The *thin curves* exhibit the modeled growth curves that were used to standardize weights to seven years of age for four arbitrarily chosen females. Note that the modeling is based on one body mass measurement per age per individual. This was carried out using curves that were specific to sex, season, and population

However, we acknowledge that our approach has weaknesses. For example, it assumes that all individuals follow the same growth pattern, but with different individual deviations from the mean, which may not be the case (Zedrosser et al. 2006), and it neglects possible senescence effects. We are aware that our comparison could have been solved using a nonlinear mixed effect model (N. G. Yoccoz, personal communication). However, we believe that our model is more pedagogical and easier to follow than a mixed model. Furthermore, our reasonably large number of observations should diminish the uncertainty in the growth curves, thus leaving the residuals approximately independent and suitable for our approach (S. Engen, personal communication). To explore the credibility of our model, we applied two approaches. First we tested it by using data from northern bears that had been weighed at ≥5 different ages in spring (the only season with sufficient data). If our model is a good predictor of body mass development, it should generate individual growth curves that give similar estimates of mass at age seven, regardless of the age of weighing. We constructed growth curves for all individual mass per age records and predicted body masses at seven years for each of them. Second, we modeled the corrected body masses using basically the same model as we used in our main analysis, but incorporating age as a factor to explore whether this would yield results that were similar to those obtained by our modeling approach.

Akaike's Information Criterion (AIC) was used to select the number of variables and interactions to be included in the final model. This was done by using stepAIC (a function in the MASS library performing stepwise model selection) in S-PLUS 6.2 (Insightful Corp. 2003). In this procedure, a stepwise algorithm performs model selection by AIC. The set of models compared ranged from the inclusion of one variable to the inclusion of all second- and third-order interactions. The stepwise search was performed both ways, which is regarded as being more robust and applicable than regular one-step approximations. We finally calculated the likelihood of the models in order to quantify the plausibility of each model and then used this information to determine the Akaike weight for each model (Burnham and Anderson 2002). This is the weight of evidence in favor of each model, given that one of the tested models must be the best model.

Results

Comparisons based on the global linear model

To test the credibility of our modeling approach, we obtained repeated measurements from 11 males and 22

females that each had their body masses recorded at ≥5 different ages in spring. The model predicted mass of bears at age 7 relatively consistently, even when masses were estimated based on the growth curves starting at different ages; males showed a greater interindividual body mass variation in the population than did females (Fig. 2). The standard deviation of the predicted masses at age seven years for individual males averaged 21.1 kg (max = 23.0 kg, min = 9.9 kg), whereas females showed less variability and had a mean standard deviation of 10.3 kg (max = 17.4 kg, min = 3.6 kg). This suggests that individual body masses for European brown bears can be described reasonably well with our modeling approach (i.e., the von Bertalanffy equation is a capable descriptor of general brown bear body mass development, and individuals follow this curve but show a relatively consistent deviation from it through life). We conclude that these results support our approach and suggest that using age-standardized body masses generated by our model will produce reasonably reliable results.

In total, we obtained body masses from 1,771 brown bears, 330 from the south and 1,441 from the north. The best fit (stepAIC) model for corrected weights evaluated at seven years included the following variables and interactions: sex + season + population + sex:season + season:population (Table 2). The models that also added the interaction sex:population and did not include sex:season were ranked with ΔAIC values <2 and were thus not considered to be significantly different in explaining variation in body mass (Burnham and Anderson 2002) (models not shown). The best-fitting global model showed that bears in the north and south did not differ in body mass when corrected for the other factors (Table 3). We also modeled body mass of the bears by using age and age^2 as a factor in addition to the same main factors as we incorporated in the previous model where age was omitted. This analysis gave the same main results as the model omitting age (Table 3), thus supporting our results based on the model that included age indirectly.

Although there was no difference in body mass between the north and south, when corrected for other factors, the model without age indicated, as expected, that body mass was larger among males (Table 3; sex, Fig. 3) and greater in autumn than in spring (Table 3; season, Fig. 3). There was a larger change in body mass between spring and autumn among females than males (Table 3; sex:season, Fig. 3), and bears in the north changed more in body mass between seasons than those in the south, where males showed no increase in body mass (Table 3; season:population, Fig. 3). Apparently, northern bears had

Fig. 2 Individual variability of expected body masses at seven years of age for 33 northern bears, where we were able to model at least five or more growth curves (per bear) based on spring body masses recorded at different ages. Mean expected body masses are shown with 95% confidence intervals
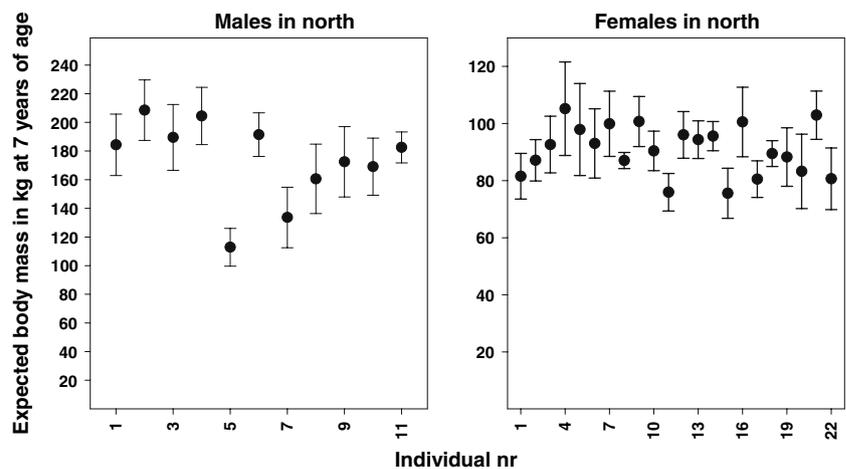
Table 2 Models entered into the stepwise procedure to find the best factors explaining variation in body mass of European brown bears, based on the Akaike information criterion (AIC)

Model description	ΔAIC	$l(g_i|x)$	w_i
Sex + season + population + sex:season + season:population	0.00	1.000	0.416
Sex + season + population + sex:season + season:population + sex:population	0.37	0.831	0.346
Sex + season + population + season:population	1.17	0.557	0.232
Sex + season + sex:season	9.42	0.009	0.003
Sex + season + population + sex:season	11.41	0.003	0.001

The likelihood ($l(g_i|x)$) for each model and its corresponding Akaike weight (w_i) is displayed to the right in the table

Table 3 Comparison of the significance of variables examined to explain the variation in body mass of brown bears in two populations in Europe (southern in the Dinara Mountains and northern in Scandinavia), based on two linear models

Model description	Variables	t value	Standard error	Estimated difference (kg)	Probability
(1) Linear model based on data from our modeling approach, encorporating age as a factor indirectly in the model	Intercept	118.3501	5.4×10^{-5}		0.000
	Population	0.4104	4.6×10^{-5}	9	0.682
	Sex	42.9479	4.5×10^{-5}	93	0.000
	Season	17.7477	5.4×10^{-5}	29	0.000
	Sex:season	13.7053	4.6×10^{-5}		0.000
	Season:population	8.2424	4.6×10^{-5}		0.000
(2) Linear model based on the basic data using age as a factor	Intercept	29.2148	1.7074		0.000
	Population	1.0293	1.0579	13	0.303
	Sex	30.4510	0.8196	50	0.000
	Season	38.4195	0.8300	65	0.000
	Age	40.2768	0.4951		0.000
	Age^2	25.7698	0.0259		0.000

The models are: (1) the best model (see Table 2) based on body masses estimated for a common age in both populations and generated by our modeling approach eliminating age as a factor, and (2) the ''control'' model based on body masses corresponding to specific ages in both populations

greater body mass during autumn than southern bears, but lower body mass in the spring.

Asymptotic (adult) body masses

The von Bertalanffy growth curves were based on fewer bears in the older age classes in the south, particularly for males. The growth curve for males in south is therefore rather uncertain, especially in the autumn. We tested for differences among asymptotic corrected body masses (i.e., adult body mass) by sex, season, and population (Fig. 3, Table 4) using z tests to help illustrate the patterns identified in the analysis.

The age at which 90% of asymptotic body mass was reached was chosen to compare the age at which adult size was attained between the two populations. For females in spring, it was six years in both the south and the north. In autumn it was five and six years, respectively. The age at which 90% of male asymptotic body mass was reached in spring was twelve years in the south and nine years in the north and in autumn it was eleven and seven years, respectively. However, the growth curves produced for southern males were relatively inaccurate, as we only had data from seven males >10 years old in the south, compared with 68 in the north.

The difference in spring and autumn asymptotic body mass for southern females was 25 kg ($z = 2.02$, $P = 0.022$, Table 4), which was a 22% increase from spring to autumn and a 18% loss from autumn to spring. Southern males did not show a significant difference between seasons ($z = 0.16$, $P = 0.44$); the asymptotic body mass for males

was actually lower in autumn than in spring (Table 4). However, as mentioned earlier, this estimate was poor for southern males.

In the north, the asymptotic body mass for females differed by 62 kg between spring and autumn ($z = 15.72$, $P < 0.001$, Table 4). This represented a 65% increase from spring to autumn and a 39% decline from autumn to spring. In northern males, the difference was 71 kg ($z = 10.11$, $P = 0.000$), or a 35% increase from spring to autumn and a 26% decline from autumn to spring.

Trends in body mass within seasons

As stated in the ''Methods'' section, we derived cubic regressions to correct for spring and autumn body masses for bears in each population (Table 5). Surprisingly, we found different trends. As expected, the bears in the north showed increasing body mass within the season for both sexes and both seasons (Table 5). In the south, however, bears of both sexes exhibited a loss of body mass in spring, but an expected gain in autumn (Table 5).

Discussion

Hypotheses predicting geographical variation in body mass

The z tests and both of the global linear models revealed no statistically significant difference in body mass between the two populations, when corrected for the other

Fig. 3 The relationship of seasonally corrected body mass to age for brown bears in southern Europe (Dinara Mountains) and northern Europe (Scandinavia) using the von Bertalanffy equation
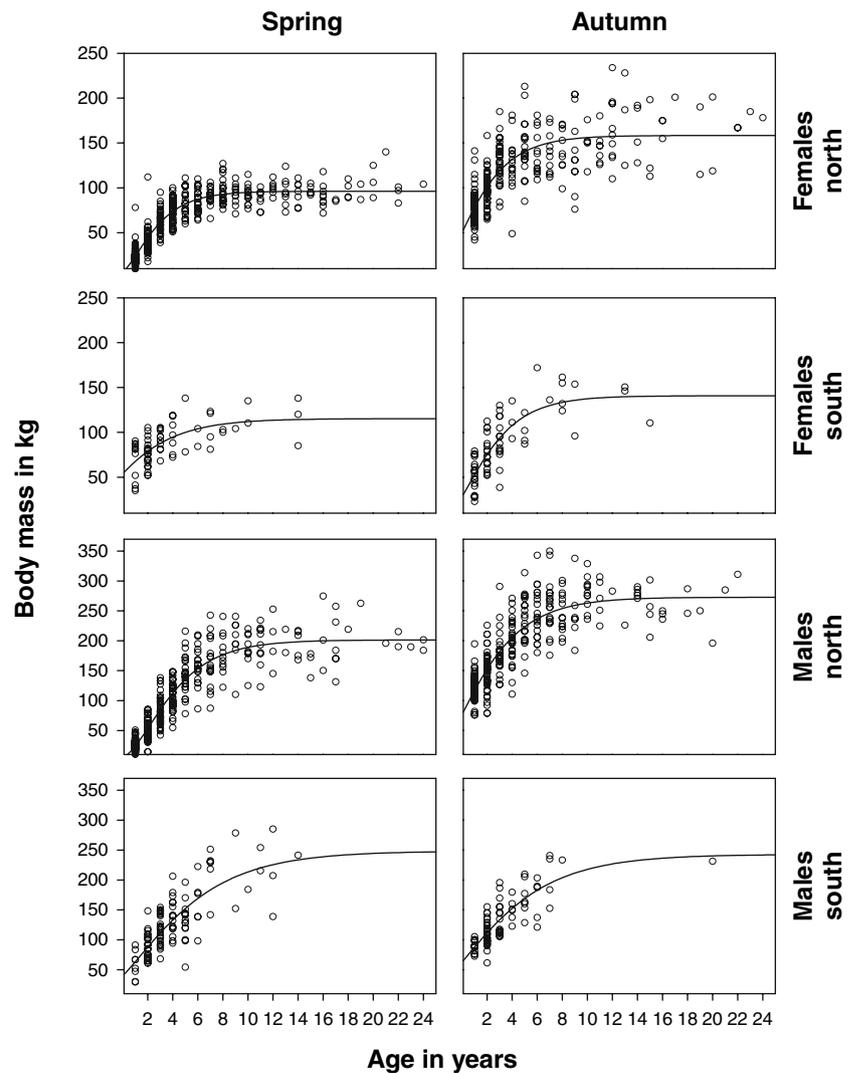

Table 4 Asymptotic body mass and growth constants (K) of brown bears from southern Europe (Dinara Mountains) and northern Europe (Scandinavia)

Population	Sex	Season	Asymptotic body mass (kg, mean ± SE)	K ± SE	N
South	Female	Spring	115 ± 8.6	0.315 ± 0.131	67
		Autumn	141 ± 9.2	0.395 ± 0.092	69
	Male	Spring	248 ± 24.9	0.223 ± 0.051	111
		Autumn	243 ± 23.9	0.232 ± 0.055	83
North	Female	Spring	96 ± 1.5	0.492 ± 0.031	446
		Autumn	158 ± 3.7	0.417 ± 0.057	281
	Male	Spring	201 ± 3.6	0.354 ± 0.017	413
		Autumn	273 ± 6.0	0.335 ± 0.032	301

factors in the models. Thus, our results did not support the hypotheses that predicted larger bears in the north (Bergmann's rule, the fasting endurance hypothesis, and the dietary meat hypothesis), nor those that predicted that bears should be larger in the south (hypotheses stressing the role of high primary productivity, high population density, low seasonality, and length of the growing season). The similarity of body masses between our southern and northern European study areas contrasts with the twofold variation in body masses of adult male and female brown bears in North America (Hilderbrand et al. 1999a). Nevertheless, a cluster analysis of combined autumn and spring adult female body masses, density and climate parameters of 24 North American brown bear populations showed that the twelve interior populations, spanning from about 65°N to about 44°N, formed one group (Ferguson and McLoughlin 2000). Our samples ranged over a similar range of latitudes, from 69°N to 44°N. The largest North American brown bears occur in the populations that feed on abundant spawning salmon (*Oncorhynchus* spp.) (Hilderbrand et al. 1999a), which does not occur in Europe.

Table 5 Trends in body mass development (in kg) within the spring and autumn seasons for brown bears in southern Europe (Dinara Mountains) and northern Europe (Scandinavia)

Population	Sex and season	Cubic regression	Trend	F	p
Southern	Males in spring	$114.4 + 26.9X – 10.7X^2 + 1.1X^3$	Decreasing	0.675	0.569
Southern	Males in autumn	$–482.2 + 111.1X – 5.0X^2$	Increasing	2.455	0.092
Southern	Females in spring	$86.7 – 10.5X + 6.1X^2 – 0.8X^3$	Decreasing	15.705	0.000
Southern	Females in autumn	$–351.8 + 62.7X – 0.2X^3$	Increasing	3.437	0.038
Northern	Males in spring	$223.6 – 44.4X + 0.2X^2 + 0.6X^3$	Increasing	2.244	0.083
Northern	Males in autumn	$1616.0 – 258.4X + 1.2X^3$	Increasing	8.267	0.000
Northern	Females in spring	$100.3 – 13.7X + 0.2X^3$	Increasing	4.237	0.015
Northern	Females in autumn	$75.1 – 2.3X + 0.1X^3$	Increasing	5.296	0.006

We used cubic regressions to correct spring and autumn body masses. Note that the quadratic or cubic parameter evaluated to zero for some of the cubic regressions. X represents the number of the month

Seasonal changes in body mass

In spite of the overall lack of difference in body mass between populations, the analyses revealed some important patterns. Although body mass was greater in autumn than spring in the global linear models, bears in the north had a greater change in body mass between seasons. Based on the analysis of asymptotic body masses, northern females gained more mass (62 kg) than southern females (25 kg) from spring to autumn. Correspondingly, adult northern females lost more mass from autumn to spring compared to southern females. The greater seasonal changes in body mass in the north compared to the south are not surprising considering that northern bears hibernate longer than southern bears. Northern bears hibernate for 5.3–6.5 months, depending on sex and reproductive category, in central Scandinavia and 6.9–7.5 months in northern Scandinavia (Manchi and Swenson 2005). In the south, however, the mean denning time is 2.9 months, and tracks and fresh scats are observed in all winter months, suggesting that many bears do not hibernate for the entire winter and that some may not hibernate at all (Huber and Roth 1997). Nondenning brown bears have also been reported from Italy (Roth et al. 1992) and Spain (Naves and Palomero 1993).

Differing trends in body mass within the spring season

Population differences were observed in body mass change during the spring season. Although the regressions with the best fit were often cubic, the trends were for increases for both sexes in the north and decreases in the south. Noyce and Garshelis (1998) challenged the existence in bears of the spring ''negative foraging period'' with declining body mass, but both increases and decreases in body mass have been reported for brown and North American black bears (*U. americanus*) in North America (Noyce and Garshelis

1998; Rode et al. 2001; Schwartz et al. 2003). The decline in mass during spring in the south occurs despite the unnatural situation of feeding of brown bears by humans in both countries. In Slovenia, the law requires one bear-feeding site per 6,000 ha in the brown bear core area (Simonič 1994), but bears also make intensive use of ungulate feeding sites stocked with corn (Große et al. 2003). Bears are not fed by humans in Sweden or Norway. An important difference between populations may be the availability of high-protein foods, because spring mass gain by brown bears is 64% lean body mass (Hilderbrand et al. 1999b). In the south, corn is available year-round (ca. 580 g/ha/year), but the availability of provided meat declines rapidly from late winter to summer (Große et al. 2003). In the north, ants are 100 times more available than in the south (Große et al. 2003), moose is an important food in spring (Dahle et al. 1998; Opseth 1998; Persson et al. 2001), and consumption of meat and insects in spring is far higher than in the south (Table 1). Although brown bears can gain mass in spring on a protein-rich forb diet (Rode et al 2001), protein digestion is higher for meat than plant diets (Pritchard and Robbins 1990). We suggest that the greater availability and use of protein-rich meat and insects in the north promotes greater mass gain in spring.

Implications for population dynamics of European bears

The global linear models showed no significant difference in body mass between the northern and southern populations, but that northern bears had more mass in autumn (which includes more fat for the longer hibernation period). An examination of Fig. 1 in Kojola and Laitala (2001) revealed that adult female body mass in autumn in Finland is similar to Scandinavia. However, female brown bears may be larger in the Carpathian Mountains. Hell (1992) reported a mean mass of 140–160 kg and a maximum of

209 kg for adult females in Slovakia, most of which had been killed in the spring. In contrast with this, the adult male mass, primarily from spring males, appears to be lower in Slovakia than in our areas, with a mean of 170–190 kg and maximum of 328 kg. The lower masses for males and higher masses for females could be the result of a Slovakian policy to avoid shooting the largest bears in order to save older males (Salvatori et al. 2002), which might have resulted in biased sampling. Greater masses have also been reported from the Romanian Carpathians, with average masses of 214 kg for females and 268 kg for males, but no further information on age or time of kill was provided, or data on whether these were especially large bears shot as trophies (Almăsan and Vasiliu 1967). Thus, we do not know if brown bears actually are larger in the Carpathians than elsewhere in Europe.

Several authors have shown that there are high correlations between female body mass and indicators of reproductive success when comparing populations (Stringham 1990a, 1990b; Hilderbrand et al. 1999a). Thus, the similar body masses in northern and southern brown bear populations in Europe suggest that they may have similar reproductive rates. The number of young that female brown bears in Scandinavia produce, ignoring mortality, has been estimated to be between 70% (northern Sweden) and 80% (southern Sweden) of the maximum rate to be expected from a brown bear population (Swenson and Sandegren 2000). Thus, the bears in southern Europe cannot reproduce at a much greater rate than those in the north. Litter sizes are similar in the north, 2.3 and 2.4 in northern and southern Scandinavia, respectively (Swenson et al. 2001) and the south, 2.4 in Croatia (Frković et al. 2001). However, there are some indications of a somewhat higher reproductive rate in southern populations. The earliest recorded ages at first birth have been five years in northernmost Scandinavia, four years in central Scandinavia, and three years in Croatia and Austria (Sæther et al. 1998; Frković et al. 2001; Zedrosser et al. 2004). The interbirth interval shows this trend as well, with 43% of the yearlings separating from their mothers in northern Scandinavia (the rest as two-year-olds), 89% in central Scandinavia, and virtually 100% in Croatia (Swenson et al. 2001; Frković et al. 2001). Similar trends have been reported for brown bears in North America (Ferguson and McLoughlin 2000).

References

Adamič M (1997) The analysis of key sources of mortality of the brown bear (*Ursus arctos* L.) in Slovenia in the last 6-year period (1.4.1991–31.3.1997). Research reports, UNI Ljubljana, Biotechnical Faculty, Ljubljana (in Slovene with English summary). For Wood Sci Technol 53:5–28

Almăsan HA, Vasiliu GD (1967) Zur Kenntnis des Rumänischen Karpatenbär. Acta Theriol 12:47–66

Atkinson SN, Ramsay MA (1995) The effects of prolonged fasting on the body composition and reproductive success of female polar bears (*Ursus maritimus*). Funct Ecol 9:559–567

Bergmann C (1847) Über die Verhältnisse der Wärmökonomie der Thiere zu ihrer Grösse. Goettinger Studien 3:595–708

Blanchard BM (1987) Size and growth patterns of the Yellowstone grizzly bear. Proc Int Conf Bear Res Manage 7:99–107

Boyce MS (1978) Climatic variability and body size variation in the muskrat (*Ondatra zibethicus*) in North America. Oecologia 36:1–19

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, Berlin

Cicnjak L, Huber D, Roth HU, Ruff RL, Vinovrski Z (1987) Food habits of brown bears in Plitvice Lakes National Park, Yugoslavia. Proc Int Conf Bear Res Manage 7:221–226

Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behaviour and ecology of two sexes. Edinburgh University Press, Edinburgh

Dahle B, Sørensen OJ, Wedul EH, Swenson JE, Sandegren F (1998) The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. Wildlife Biol 4:147–158

Dahle B, Swenson JE (2003) Home ranges in adult Scandinavian brown bears *Ursus arctos*: effect of population density, mass, sex, reproductive status and habitat type. J Zool 260:329–335

Derocher AE, Stirling I (1994) Age-specific reproductive performance of female polar bears (*Ursus maritimus*). J Zool London 234:527–536

Derocher AE, Stirling I (1996) Aspects of survival in juvenile polar bears. Can J Zool 74:1246–1252

Derocher AE, Stirling I (1998) Geographic variation in growth of polar bears (*Ursus maritimus*). J Zool London 245:65–72

Derocher AE, Wiig Ø (2002) Postnatal growth in body length and mass of polar bears (*Ursus maritimus*) at Svalbard. J Zool London 256:343–349

Elgmork K, Kaasa J (1992) Food habits and foraging of the brown bear (*Ursus arctos*) in central south Norway. Ecography 15:101–110

Ferguson SH, McLoughlin PD (2000) Effect of energy availability, seasonality, and geographic range on brown bear life history. Ecography 23:193–200

Friebe A, Swenson JE, Sandegren F (2001) Denning chronology of female brown bears in central Sweden. Ursus 12:37–46

Frković A, Huber D, Kusak J (2001) Brown bear litter sizes in Croatia. Ursus 12:103–105

Fujita R (2000) Bait-hunting for brown bear in Sweden: temporal and spatial occurrence and potential effects on the population. Undergraduate thesis, Swedish University of Agricultural Sciences, Uppsala

Große C (1999) Ants—an important food for brown bears (*Ursus arctos*) in Slovenia? Diploma thesis, Phillips-University of Marburg, Germany

Große C, Kaczensky P, Knauer F (2003) Ants: a food source sought by Slovenian brown bears (*Ursus arctos*)? Can J Zool 81:1996–2005

Hell P (1992) Biometrie und Bewirtshaftung der Population des Braunbären im Slowakischen Teil der Westkarpaten. In: F. Bourlière (President of the Scientific Committee) Management and restoration of small and relictual bears populations. Museum d'Historie Naturelle, Grenoble, France, pp 143–153

Hilderbrand GV, Jenkins SG, Schwartz CC, Hanley TA, Robbins CT (1999b) Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can J Zool 77:1623–1630

Hilderbrand GV, Schwartz CC, Robbins CT, Hanley TA (2000) Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. J Wildlife Manage 64:178–183

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C (1999a) Importance of dietary meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Can J Zool 77:132–138

Huber D, Frković A (1993) Brown bear management in Croatia. Proc Cong Int Union Game Biol 21(1):287–292

Huber D, Roth HU (1993) Movements of European brown bears in Croatia. Acta Theriol 38:151–159

Huber D, Roth HU (1997) Denning of brown bears in Croatia. Proc Int Conf Bear Res Manage 9(2):79–83

Insightful Corp. (2003) S-PLUS 6.2.Insightful Corp., Seattle, WA. http://www.insightful.com/support/splus62win/. Cited 16 March 2007

Kingsley MCS, Nagy JA, Reynolds HV (1988) Growth in length and weight of northern brown bears: differences between sexes and populations. Can J Zool 66:981–986

Kojola I, Laitala HM (2001) Body size variation of brown bear in Finland. Ann Zool Fennici 38:173–178

Laws RM (1956) Growth and sexual maturity in aquatic mammals. Nature 178:193–194

Lindstedt SL, Boyce MS (1984) Seasonality, fasting endurance, and body size in mammals. Am Nat 125:873–878

Mahoney SP, Virgl JA, Mawhinney K (2001) Potential mechanisms of phenotypic divergence in body size between Newfoundland and mainland black bear populations. Can J Zool 79:1650–1660

Manchi S, Swenson JE (2005) Denning behavior of male Scandinavian brown bears (*Ursus arctos*). Wildlife Biol 11:123–132

Matson GM, Van Daele L, Goodwin E, Aumiller L, Reynolds H, Hristienko H (1993) A laboratory manual for cementum age determination of Alaska brown bear PM1 teeth. Alaska Department of Fish and Game/Matson's Laboratory, Milltown, MT

Mayr E (1956) Geographical character gradients and climatic adaptation. Evolution 10:105–108

McLellan B (1994) Density-dependent population regulation of brown bears. In: Taylor M (ed) Density-dependent population regulation in black, brown, and polar bears. Int Conf Bear Res Manage Monogr Ser 3:15–24

McNab BK (1971) On the ecological significance of the Bergmann's rule. Ecology 52:845–854

McNab BK (1989) Basal rate of metabolism, body size and food habits in the order Carnivora. In: Gittleman JL (ed) Carnivore behaviour, ecology and evolution. Cornell University Press, Ithaca, NY, pp 335–354

Naves J, Palomero G (1993) Brown bear hibernation ecology in the Cantabrian Mountains. In: Naves J, Palomero G (eds) El oso pardo (*Ursus arctos*) en España. Instituto Nacional para la Conservacion de la Naturaleza, Madrid (in Spanish with English summary), pp 147–181

Noyce KV, Garshelis DL (1998) Spring weight changes in black bears in northcentral Minnesota: the negative foraging period revisited. Ursus 10:521–531

Opseth O (1998) Brown bear (*Ursus arctos*) diet and predation on moose (*Alces alces*) calves in the southern taiga zone in Sweden. Cand Sci Thesis, Norwegian University of Science and Technology, Trondheim

Persson IL, Wikan S, Swenson JE, Mysterud I (2001) The diet of the brown bear in the Pasvik, Valley, northeastern Norway. Wildlife Biol 7:27–37

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Pritchard GT, Robbins CT (1990) Digestive and metabolic efficiencies of grizzly and black bears. Can J Zool 68:1645–1651

Rode KD, Robbins CT, Shipley LA (2001) Constraints on herbivory by grizzly bears. Oecologia 128:62–71

Rogers L (1976) Effects of mast and berry crop failure on survival, growth, and reproductive success of black bears. Tans North Am Wildlife Nat Resour Conf 41:431–438

Rosenzweig ML (1968) Net primary productivity of terrestrial communities: prediction from climatological data. Am Nat 102:67–74

Roth HU, Boscagli G, Gentile L (1992) Movements, activity and hibernation of brown bears in the Abruzzo National Park as revealed by radiotelemetry. In: Bourlière F (ed) Management and restoration of small and relictual bears populations. Museum d'Historie Naturelle, Grenoble, France

Samson C, Huot J (1995) Reproductive biology of female black bears in relation to body mass in early winter. J Mammal 76:68–77

Sæther BE, Engen S, Swenson JE, Bakke Ø, Sandegren F (1998) Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates. Oikos 83:403–416

Sadleir RMFS (1969) The ecology of reproduction in wild and domestic mammals. Methuen, London

Salvatori V, Okarma H, Ionescu O, Dovhanych Y, Find'o S, Boitani L (2002) Hunting legislation in the Carpathian Mountains: implications for the conservation and management of large carnivores. Wildlife Biol 8:3–10

Schwartz CC, Franzmann AW (1991) Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monogr 113

Schwartz CC, Miller SD, Haroldson MA (2003) Grizzly bear. In: Feldhamer GA, Thompson BC, Chapman JA (eds) Wild mammals of North America: biology, management, and conservation, 2nd edn. John Hopkins University Press, Baltimore, MD, pp 556–586

Simonič A (1994) The legal protection of the brown bear in Slovene territory—past and present, and some suggestions for the future. In: Adamič M (ed) Rjavi medved v deželah Alpe-Adria. Gozdarski inštitut Slovenije, Ministrostvo za kmetijstvo in gozdarstvo, Republike Slovenije. Ljubljana, Slovenia, pp 43–75

SPSS Inc. (2004) SPSS Release 13.01. SPSS Inc., Chicago, IL. http://www.spss.com/. Cited 16 March 2007

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Stearns SC, Koella J (1986) The evolution of phenotypic plasticity in life history traits: predictions from norms of reaction for age- and size-at-maturity. Evolution 34:893–913

Stringham SF (1990a) Black bear reproductive rate relative to body weight in hunted populations. Proc Int Conf Bear Res Manage 8:425–432

Stringham SF (1990b) Grizzly bear reproductive rate relative to body size. Proc Int Conf Bear Res Manage 8:433–443

Swenson JE, Dahle B, Sandegren F (2001) Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. Ursus 12:81–91

Swenson JE, Sandegren F (2000) Conservation of European brown bear populations: experiences from Scandinavia. In: Layna JF, Heredia B, Palomero G, Doadrio I (eds)La conservación del oso pardo en Europa: un reto de cara al siglo XXI (Serie encuentros I). Fundación Biodiversidad, Ministerio de medio ambiente, Madrid, Spain, pp 111–116

Swenson JE, Sandegren F, Bjärvall, Söderberg A., Wabakken P, Franzén R (1994) Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. Biol Conserv 70:9–17

Swenson JE, Sandegren F, Söderberg A, Franzén R (1995) Estimating the total weight of Scandinavian brown bears from field-dressed and slaughter weights. Wildlife Biol 1:177–179

Von Bertalanffy L (1938) A quantitative theory of organic growth (Inquiries on growth laws II). Human Biol 10:181–213

Zedrosser A, Dahle B, Swenson JE (2006) Population density and food conditions determine adult female size in brown bears. J Mammal 87:510–518

Zedrosser A, Rauer G, Kruckenhauser L (2004) Early primiparity in brown bears. Acta Theriol 49:427–432