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Body size variation of brown bear in Finland

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Brown bear (*Ursus arctos*) can be predicted to have larger autumn body mass in the north than south because the duration of winter dormancy lengthens towards the north. We examined variation of body size among hunter-killed female and male brown bears within a latitudal range of 60 and 68°N in Finland. The body size of males (mass, contour length) decreased towards the north while our data did not indicate such a trend in females. Our results do not coincide with Bergmann's rule suggesting increasing body size with decreasing ambient temperature, probably owing to energy-saving winter dormancy during which brown bear is not overtly exposed to weather conditions. Secondly, possible differences in the quality of green forage might not largely influence the nutrition of an omnivorous mammal.

Introduction

Body size is associated with many regional life history features in bears, e.g. the age of first reproduction and litter size (Garshelis 1994, McLellan 1994, Ferguson & McLoughlin 2000). Well-known Bergmann's (1847) rule states that warm-blooded vertebrates within the geographical range of the species tend to be larger in cool than in warm climates (Mayr 1956), while Rozenweig (1968), predicting relationships different from Bergmann's rule, suggested that primary productivity of the environment could be positively correlated with the body size. Nutrition has been suggested to be the major factor producing differences in size, mass and growth patterns in brown bear *Ursus arctos* (Rogers *et al*. 1976, Blanchart 1987). Brown bear is an omnivorous mammal that spends winter in energy-saving dormancy. Therefore, trend in body size with increasing coldness of climate may differ from that of large herbivorous mammals which can be larger in higher altitudes (Albon & Langvatn 1986, Albon & Langvatn 1992) or latitudes (Sand *et al*. 1995). The range in latitudal gradient can be noteworthy, and above 60–65°N several terrestrial large mammals can grow smaller in size (Geist 1986). In his review based on skull measurements with North American brown bear, McNab (1971) did not find statistically significant associations between latitude and size within three latitudal ranges (30–45, 46–60 and > 60°N). This does not, however, mean that body mass will not show a latitudal

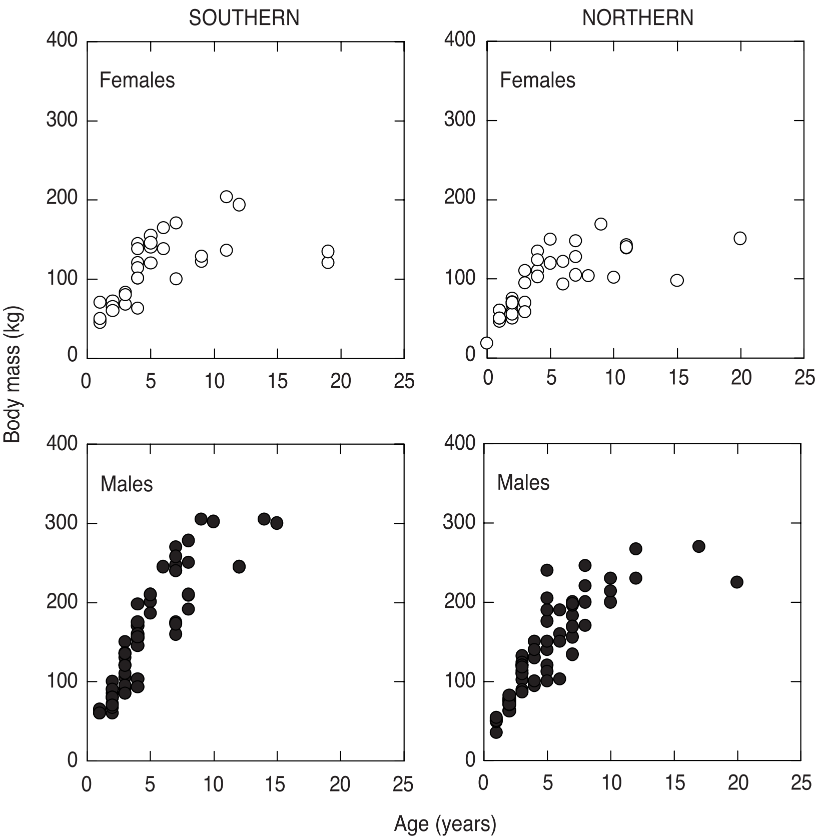

Fig. 1. The relationship between age and body mass of female and male brown bears shot in southern and northern parts our study area in Finland.

trend, because structural size can be more fixed than body mass (Dobson 1992, Sand *et al.* 1995).

Growth patterns of female and male brown bears are different. Males continue their growth longer than females, especially regarding their mass (Kingsley *et al.* 1988). Body mass might be associated with reproductive success among both sexes. Access to receptive females is probably correlated positively with the body mass among males, and the age of the first reproduction and a litter size may be connected with the body size among females (Le Boeuf 1974, Samson & Huot 1995). Geographic patterns in sexual dimorphism may provide insights into the environmental constraints that influence sexual dimorphisms (Dobson & Wigginton 1996). Herein, we examine how the body sizes of females and males in a highly polygamous mammal, brown bear, is associated with latitude and the duration of the growing season within latitudal range of 60–68°N in northwestern Europe. Although dormancy in winter dens hinders overt exposion to ambient temperatures during critical season, we may expect bears to accumulate most body reserves in north as an adaptation to longer period of fasting (Lindstedt & Boyce 1984).

Material and methods

We investigated data on 226 brown bears (82 females, 144 males) killed by hunters in Finland in 1996–1999 between the latitudes of 60 and 68°N. The study area is boreal a coniferous forest (Ahti *et al.* 1968) and kill sites were strongly concentrated close to the Finnish–Russian borderline (*see* Kojola & Laitala 2000). Brown bear in our study area belong to one mitochondrial DNA lineage (*see* Taberlet & Bouvert 1994). Bears were weighed either for total weight, field dressed mass or dressed mass by hunters, meat buyers or staff working in Finnish Game and Fisheries Research Institute at Ahvenjärvi, Ilomantsi. When the total mass was not measured, we estimated the total mass (kg) from field dressed mass or dressed mass (definitions by Langvatn 1977) according to the regression formulas given by Swenson *et al.* (1995): total mass = 4.01 + 1.16 × (field dressed mass), total mass = 4.63 + 1.49 × (dressed mass). A contour length (distance from the base of tail to tip of nose with measuring tape following dorsal contour) was measured in 177 animals (67 females, 110 males). All these bears were weighed also for body mass. The shot bears were aged by counting the cementum annuli from tooth at Matson's laboratory, Montana, and date and location (N and E coordinates) for kills were recorded.

We extracted the duration of the growing season for each bear from the isoclines produced by Finnish Meteorological Office. Bear kill sites ranged between 120 and 170 days. The effective temperature sums (day degrees, °C) of kill sites were closely correlated (r = 0.96) with the duration of the growing season. The relationships of the mass and the contour length to the age were nonlinear and after transformations of each of these variables into natural logarithms they were used in linear models.

We tested the difference in ln(body mass) between the southern and northern parts of our study area with ANOVA with ln(age) as a covariate. We performed multiple linear regressions with the body mass or the countour lengths as an independent variable, separately for the females and males. To assess whether interactions between sex on the body mass or the contour length do exist we carried out general linear models (GLM). In all statistical analyses, we used SYSTAT statistical package, and all the reported probabilities are two-tailed.

Results and discussion

The asymptotic body mass (*see* e.g. Kingley *et al.* 1988) could not be assessed for the males from the southern part of our study area (< median latitude, 62°41´N) because the relationship between the age and mass remained almost linear within the range of ages in the south (1–15 years, Fig. 1). Anyway, brown bear achieved higher body mass in the southern than in the northern parts of our study area while such a difference was not evident among females (Fig. 1). The difference between the northern and southern parts was significant among the males (ln(body mass), F = 16.66, df = 1, 125, P < 0.001, ln(age) as a covariate), but not among the females (F = 2.17, df = 1,64, P = 0.146). The duration of the growing season was associated with male body mass while not female body mass (Table 1). Significant interactions existed between sex and age, and sex and the duration of the growing season on body mass (Table 2). Only the male countour length was associated with the growing season (Table 3), while the GLM model did not indicate that sex and the duration of the growing season had any significant effect on the contour length (t = 0.37, P = 0.713). When analyses of body mass were restricted only to cases where the countour length was measured (n = 53 females, 99 males), only the male body mass was still associated with the duration of the growing season (Table 3), while

Table 1. The effects of age (years) and the duration of the growing season (days) on body mass (kg) of female and male brown bears in Finland.

Sex	Dependent variable	Independent variable	Intercept	Regression coeffiecient	Student's t	P
Female	Ln (mass)	Ln (age)	1.67	0.41	12.00	< 0.001
		Growing season		0.00	0.46	0.649
		F = 73.42, r^2 = 0.68, P < 0.001				
Male	Ln (mass)	Ln (age)	1.27	0.68	27.34	< 0.001
		Growing season		0.00	4.84	< 0.001
		F = 380.78, r^2 = 0.86, df = 2,125, P < 0.001				

interaction between the age and duration of the growing season on the body mass was not quite significant in this subset of the data (t = 1.76, P = 0.080).

Our results were not in agreement with predictions derived from fasting endurance hypothesis (Lindstedt & Boyce 1984) which suggests increasing accumulation of body reserves in harsher environments. Through dormancy in dens, brown bears are not overtly exposed to ambient temperatures in winter which might level down the influence of weather conditions on energy expenditure. Dormancy in dens could thereby decrease the effects of the coldness and/or unpredictability of the climate which have been suggested to be the primary agents of selection for large body size, owing to increased fasting endurance during periodes of food shortage in seasonal environments (Linstedt & Boyce 1985, Millar & Hickling 1990).

Climatic conditions might influence latitudal variation in the body mass also indirectly, through the biomass and nutritional value of plant forage (Demment & Van Soest 1985). These variables may even have opposite trends with increasing latitude. Although primary productivity is higher in southern Finland (Koivisto 1970), forage quality may be better in climatically harsher environments (Albon & Langvatn 1992). In ungulates, nutritional quality can outweigh the effects of plant biomass on body mass (Geist 1986, Langvatn & Albon 1986). Although a geographical gradient in nutritional quality of browse might explain, for example, why body mass of Swedish moose (*Alces alces*) increases with latitude (Sand *et al*. 1995), starting points for brown bear are different from those with large herbivores, due to omnivory and characteristics of the seasonal diet. Both in the southern and the northern study areas in Sweden, ungulates predominate in the spring (March–May) and berries in the autumn (August–October) and even in the summer (June–July) diets of brown bear, when greens are most important greens

Table 2. The effects of age (years), sex, the duration of the growing season, their two-way interactions on body mass of brown bear in Finland.

Dependent variable	Independent variable	Intercept	Regression coefficient	Student's t	P
Ln (body mass)	Ln (age)	2.26	0.00	0.89	0.372
	Sex		0.39	2.43	0.021
	Growing season		0.00	1.58	0.116
	Sex × ln (age)		0.27	6.67	< 0.001
	Sex × growing season		0.00	2.17	0.031
	Ln (age) × growing season		0.00	1.50	0.136
	F = 157.66, adjusted r^2 = 0.83, P < 0.001				

Table 3. The effects of age (years) and the duration of the growing season (days) on countour length (cm) of female and male brown bears in Finland.

Sex	Dependent variable	Independent variable	Intercept	Regression coefficient	Student's t	P
Female	Ln (contour length)	Ln (age)	1.96	0.17	22.23	< 0.001
		Growing season		0.00	1.23	0.224
		F = 62.71, r^2 = 0.70, df = 2,50, P < 0.001				
Male	Ln (contour length)	Ln (age)	1.95	0.22	35.86	< 0.001
		Growing season		0.00	2.48	0.015
		F = 154.94, r^2 = 0.76, df = 2,96, P < 0.001				

constitute only ca. 20% of the estimated dietary energy content (*see* Dahle *et al*. 1998). The mass gain in male brown bears seemed to be limited by duration of the growing season, primary productivity or moose density. The density of the most important ungulate prey of brown bear, moose (*see* Dahle *et al*. 1998), decreases in our study area from south to north (Danilov *et al*. 1996).

Although our analysis provided evidence that the body mass of the females is less influenced by the latitude than that of the males, we cannot draw the conclusion that, for example, the duration of the winter sleep does not have any impact on the female body mass in Finnish brown bear because the probability of a type II error (undetected significant difference) greatly depends on sample size (Peterman 1990). The observed indications, anyhow, suggested that the female body size was more fixed than that of males. Possible explanations remain speculative. Although litter size is smaller and interbirth interval longer, for example, in northern than southern Scandinavia (Saether *et al*. 1998), we did find evidence to suggest that the duration of the growing season affects reproductive effort more by females than males.

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