Correlates with body size and mass in yearling brown bears (*Ursus arctos*)

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Abstract

Body size and mass have a strong effect on an individual's fitness, and conditions experienced early in life may affect survival to adulthood, age and size at maturation, and reproductive success. For this reason, body size and mass of 226 yearling brown bears *Ursus arctos* were analysed in relation to maternal size, litter size, sex, multilocus heterozygosity, population density and cohort in two study areas in Sweden. Body mass of yearlings varied from 8 to 48 kg ($\bar{X} = 24.5 \pm 0.5$sE). Yearling body size and mass were positively related to maternal size and negatively related to litter size. Males were on average 2.6% larger and 7.8% heavier than females. Population density negatively affected both size and mass of yearlings. Yearling body size and mass varied among cohorts, but data on food availability were not available to evaluate the relationship between food availability and size and mass of yearlings. Maternal age and multilocus heterozygosity did not seem to influence yearling body size or mass. Body mass of yearlings varied within litters, especially in litters with three offspring, where the heaviest yearling was on average $29.5 \pm 2.8\%$ (sE) heavier than the lightest one. This suggests that competition among offspring increases with litter size, thereby having a pronounced negative effect on the smallest offspring. Survival of subadult brown bears from ages 1 to 3 increased with increasing yearling body size.

Introduction

Body mass is one of the most important factors affecting an individual's fitness. Body mass at birth or weaning is usually positively associated with early survival (e.g. Winters, Cummings & Stewart, 1947; Haukioja & Salovaara, 1978; Baker & Fowler, 1992; Festa-Bianchet *et al.*, 1997) and even with survival to adulthood (e.g. Albon, Clutton-Brock & Guinness, 1987). Additionally, body mass at birth or weaning is reported to be positively correlated with body mass later in life (Schultz & Johnson, 1995; Birgersson & Ekvall, 1997), size as adults (Myers & Master, 1983; Albon *et al.*, 1987; Festa-Bianchet, Jorgenson & Reale, 2000) and lifetime reproductive success (Festa-Bianchet *et al.*, 2000; Steinheim *et al.*, 2002). Thus, conditions experienced during early development can influence growth, survival and later reproduction in birds and mammals (Lindström, 1999; Solberg *et al.*, 2004). Body mass measurements of offspring just before separation from their mothers vary considerably in many species, e.g. alpine marmots *Marmota marmota* (Allaine, Graziani & Coulon, 1998) and polar bears *Ursus maritimus* (Derocher & Stirling, 1998*a*). It is important to understand the variation in body mass, because it may have a pronounced effect on survival and reproductive success.

In this paper we analyse the size and mass of yearling brown bears *Ursus arctos* in Sweden collected during a 14-year period. The brown bear has a circumpolar distribution and inhabits habitat types ranging from tundra and boreal forest to temperate deciduous forests (Servheen, Herrero & Peyton, 1999). Age at first reproduction (4–8 years), litter size (1–4 cubs born in January) and length of maternal care (1.4–3.5 years) vary among populations and are linked to body size and condition, which in turn are linked to nutrition (Stringham, 1990; Hilderbrand *et al.*, 1999; Dahle & Swenson, 2003*a*). In brown bears reproductive longevity was thought to approximate physical longevity (Pasitchniak-Arts, 1993), but new data presented by Schwartz *et al.* (2003) suggest that reproductive senescence occurs approximately at the age of 27. Body mass of vertebrates is a function of both skeletal size and body condition (both muscles and stored fat). Brown bears exhibit large seasonal fluctuations in body mass because they store adipose tissue during summer and fall for winter hibernation (Hilderbrand *et al.*, 2000). For this reason we analysed skeletal size (hereafter body size) and body mass separately, although most previous studies have focused only on body mass. We measured the brown bears at yearling age and not as cubs-of-the-year for ethical reasons,

because capturing females with cubs-of-the-year might cause separations of mother and offspring, resulting in the death of cubs-of-the-year. On the basis of the available literature, we considered seven factors that are likely to affect body size and mass of yearling brown bears. The predictions are summarized in Table 1.

Maternal size

Larger females may produce larger and heavier offspring (Myers & Master, 1983; Clutton-Brock, Albon & Guinness, 1988; Wauters, Bijnens & Dhondt, 1993; Arnbom, Fedak & Boyd, 1997) and offspring of larger mothers may show increased pre-weaning growth (Myers & Master, 1983; Arnbom *et al.*, 1997; Barbraud *et al.*, 1999). Most studies have used maternal mass as the maternal trait (e.g. Derocher & Stirling, 1998*a*; Bowen *et al.*, 2001). Body mass is very dependent on the amount of adipose tissue in bears (Ramsay & Stirling, 1988; Hilderbrand *et al.*, 2000), and to be most meaningful as a maternal trait, maternal mass should be measured at implantation (in late fall) or at birth (during hibernation in January). Because of ethical reasons (to avoid drowning and overheating) and for practical reasons (ease of capture), bears were captured in early spring when the ground was still snow covered. For these reasons we used maternal size, which is not dependent on capture date, as the maternal trait in the analyses. We predicted (1) a positive relationship between maternal size and yearling size and mass (Table 1).

Maternal age

In mammals, measurements of reproductive performance (e.g. litter size and offspring mass) initially increase and then remain constant or decline as the animals age (Clutton-Brock, 1984; Sydeman *et al.*, 1991; Hewison & Gaillard, 2001). Reproductive senescence has been reported for

female brown bears (Schwartz *et al.*, 2003), but possible relationships between maternal age and other reproductive parameters have not been reported in brown bears. Derocher & Stirling (1994) found that litter mass and litter size in polar bears followed a curvilinear relationship with maternal age, and Derocher & Stirling (1998*a*) reported that offspring size increased from the onset of reproduction before subsequently decreasing from the age of 15 years. On the basis of this we predicted (2) that yearling size and mass should increase to a certain maternal age and thereafter decrease (Table 1).

Litter size

Life-history theory predicts a compromise between the number and size of offspring (Smith & Fretwell, 1974), and such a negative relationship has been reported in a wide variety of taxa (for reviews see Lloyd, 1987; Roff, 1992). Thus we predicted (3) a negative relationship between litter size and yearling body size and mass (Table 1).

Gaillard *et al.* (1998) reported that variation in growth within litters increased with litter size in roe deer *Capreolus capreolus*. In polar bears, Derocher & Stirling (1998*a*) found that the difference in body mass between siblings in triplet litters was *c*. 3–6 times larger than that found in twins. They argued that the disparity in mass of individuals in triplets might represent competition among siblings for milk, because mothers may be constrained in their ability to control the variation in offspring size. On the basis of the findings of Derocher & Stirling (1998*a*) and Gaillard *et al.* (1998), we predicted (4) that variation in offspring size and mass within litters increases with increasing litter size (Table 1).

Sex

It is generally accepted that in species where the variance in reproductive success is greater in one sex and where parental investment influences reproductive success, parents should invest more in the sex with the highest variance in reproductive success, which in polygynous species usually is the male (Trivers, 1972; Maynard-Smith, 1980). A critical assumption for the sex-allocation hypothesis is that a significant part of the variance in male reproductive success can be subscribed to parental investment. This assumption often remains untested as individuals must be followed from birth to adulthood to monitor to what extent increased parental investment increases offspring survival to adult age, and to what extent a size advantage at weaning resulting from increased parental investment persists into adulthood. Adult male brown bears are on average twice as heavy as females and body size and mass positively affect male mating success (Bellemain *et al.*, 2006), as is reported for other polygynous species (e.g. McElligott *et al.*, 2001). In brown bears, little is known about the relationship between male body size and mass early in life and in adulthood, but the relationship seems to be non-significant in females (Zedrosser, Dahle & Swenson, in press). The critical assumption that a significant part of the variance in male reproductive success can be

Table 1 Summary of predictions

Prediction	Supported
1. A positive relationship between maternal size and yearling size and mass	Yes
2. Yearling size and mass increases to a certain maternal age and thereafter decreases	No*
3. A negative relationship between litter size and yearling size and mass.	Yes
4. Variation in offspring size and mass within litters increases with increasing litter size	Yes
5. Males are larger and heavier than females, both within and among litters	Yes
6. A positive relationship between multilocus heterozygosity and yearling size and mass	No
7. Yearling size and mass are inversely related to population density	Yes
8. Size and mass of yearlings differ among cohorts	Yes
9. Subadult survival (1–3 years old) is positively related to yearling size and mass	Yes

*Limited support.

subscribed to maternal investment therefore remains untested. If this assumption holds, the sex-allocation hypothesis predicts (5) that maternal expenditure per individual offspring should be higher for males than females, and yearling males should be larger and heavier than females, both within and among litters (Table 1). However, we acknowledge that there are competing hypotheses to explain why males should be larger and heavier than females at this age.

Multilocus heterozygosity

Several hypotheses suggest a correlation between genetic heterozygosity and fitness-related traits in natural populations (for a review see Hansson & Westerberg, 2002). Significant multilocus heterozygosity (the number of heterozygous loci)–fitness correlations have been found in fish (e.g. Thelen & Allendorf, 2001), birds (e.g. Hansson *et al.*, 2001), and mammals (e.g. Coltman, Bowen & Wright, 1998), including male mating success in brown bears (Bellemain *et al.*, 2006). Coltman *et al.* (1998) examined the relationship between fitness-related traits and microsatellite heterozygosity in wild harbour seal pups *Phoca vitula*. They found that birth mass was positively influenced by maternal age, pup sex and individual heterozygosity. We predicted (6) a positive relationship between multilocus heterozygosity and yearling body size and mass (Table 1).

Population density

In general, an increase in population density will increase competition for food. This might result in a decrease in body mass, as has been reported in ungulates (e.g. Gaillard *et al.*, 1996; Hjeljord & Histøl, 1999) and birds (e.g. Cooch *et al.*, 1991) and also suggested for bears from interpopulation comparisons (Nagy & Haroldson, 1990; McLellan, 1994; Derocher & Wiig, 2002). Our populations 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 & Drageset, 2003), suggesting that the population was near or approaching carrying capacity. In line with this, Zedrosser *et al.* (in press) found that the size of adult female brown bears decreased with increasing population density in our study populations. Maternal expenditure generally decreases under adverse environmental conditions (Reale, Bousses & Chapuis, 1999; Adams, 2005). We would therefore expect that an increase in population density should increase competition for food resources, which may result in decreased maternal expenditure, because food resources should be more limited when the population approaches carrying capacity. Thus, using estimates of population density surrounding individual bears, we predicted (7) that yearling body size and mass should be inversely correlated with population density (Table 1).

Cohort

Changing food availability among years might have a pronounced effect on maternal condition and the transfer of resources from mother to offspring, thus affecting offspring growth rate and body mass (e.g. Ono, Boness & Oftedal, 1987; Allaine *et al.*, 1998). Additionally, brown bear cubs-of-the-year feed on solid food, especially after the lactation peak around mid-summer (Farley & Robbins, 1995). Preliminary analyses suggest that yearling body mass differs among cohorts (Swenson, Dahle & Sandegren, 2001*a*). Availability of berries varies among years in the boreal forest as does brown bear food habits (Nilsen, 2002). For this reason we predicted (8) that body size and mass of yearlings should differ among cohorts (Table 1).

Life-history effects of size and mass

To evaluate the life-history effect of size and mass, we also analysed juvenile survival. Early survival (Winters *et al.*, 1947; Haukioja & Salovaara, 1978; Baker & Fowler, 1992; Derocher & Stirling, 1996) and survival to adulthood (Albon *et al.*, 1987; Festa-Bianchet *et al.*, 1997) are generally positively associated with offspring size and mass. Therefore we predicted (9) that subadult survival (1–3 years old) should be positively related to yearling body size and mass (Table 1).

Methods

Study areas

The study was performed in Dalarna and Gävleborg counties in south-central Sweden (*c.* 61°N, 14°E, southern study area), and in Norbotten County, northern Sweden (*c.* 67°N, 18°E, northern study area) in 1989–2002. Both areas are close to the northern and southern edges of the range of the Scandinavian brown bear population and are *c.* 600 km apart. The southern study area (south) consists of 13 000 km² of intensively managed boreal forest in a rolling landscape. The forest is dominated by Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, but deciduous trees like mountain birch *Betula pubescens*, silver birch *Betula pendula*, aspen *Populus tremula* and grey alder *Alnus incana* are common. The elevations range from about 200 m a.s.l. in the south-eastern part to about 1000 m a.s.l. in the western part, but only a minority of the area is above timberline, which is about 750 m a.s.l. The mean temperatures in January and July are −7 and 15 °C, respectively. Snow cover lasts from late October/early November until early May and the vegetation period is about 150–180 days (Moen, 1998). Average precipitation is ∼600–1000 mm annually (Lundqvist, 2002). Bears are hunted in the entire area.

The northern study area (north) encompasses 8000 km² 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 2000 m. The valleys are dominated by mountain birch, Scots pine and Norway spruce. Mountain birch forms the treeline and occurs at a maximum elevation of 600 m a.s.l (Grundsten, 1997). The mean temperatures in January and July are −13 and 13 °C, respectively. Snow cover lasts from the beginning of October until late May, and the vegetation period is about 110–130 days (Moen, 1998). Average precipitation is ∼500–1000 mm annually (Påhlson, 1984). In the south, 95% of the litters are weaned as yearlings (Dahle & Swenson, 2003b), whereas only 53% of the litters are weaned as yearlings in the north (Dahle & Swenson, 2003a). Because of the differences between the study areas, we controlled for study area in the analysis.

Capture and handling

Yearling brown bears and their mothers were immobilized 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 tiletamine, 2.5 mg zolazepam and 0.02 mg medetomidine per kg to immobilize the bears. Atipamezol was used as an antidote for medetomidine (5 mg per 1 mg medetomidine; Kreeger, Arnemo & Raath, 2002). The age of offspring was known for most captured young from the reproductive pattern of the radio-marked mother. The age of offspring from unmarked mothers was determined from tooth eruption patterns (Jonkel, 1993) From adult individuals of unknown age, the first premolar was extracted and sent to Matson's, Inc., Milltown, Montana, for age determination by counting cementum annual layers (Craighead, Craighead & McCutchen, 1970). The body mass of immobilized bears was measured with a scale, and the head circumference (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. Head circumference should reflect skeletal dimensions, independent of body condition, because fat deposition on the head is small (Derocher & Stirling, 1998b), especially after winter hibernation. Because the bears were captured within a 2-week period in each study area, we did not adjust body size or mass for capture date. Until 1998, almost all yearlings were equipped with radio-transmitters attached to neck collars (Telonics model 400; Telonics, Meza, Arizona, USA). Radio-collared subadult brown bears were tracked in order to estimate their survival. Subadult bears were recaptured every spring to replace the radio-collar with a larger one. On collars placed on subadult bears, a break-away section made of canvas was added in case we were not able to recapture the individual because of radio-failure. On adult bears, collars were replaced every second to every third year. Neck collars were removed when the individual was no longer followed by the project.

Relative population density index

The population density around each individual (within a radius of 17.84 km, which corresponds to the density of bears per 1000 km^2) was estimated in both the north and the south based on the high proportion of radio-marked bears and documented population growth rates [see Zedrosser et al. (in press) for a more detailed description]. In the south, the population size was estimated on the basis of a DNA analysis of scats collected throughout the area in 2001 and 2002 (Bellemain et al., 2005). The individual density index around each radio-marked individual in our analysis was based on the location of individuals genetically identified by the scat sampling, the location of the radio-marked bears (71% of the radio-marked bears were represented in the scat samples; Bellemain et al., 2005) and the population growth rate (Sæther et al., 1998), which we used to temporally correct the density estimate. No corresponding population estimate was available for the north, but virtually every adult male and female and all subadult female bears were radio-marked (Swenson et al., 2001b). We used the locations of radio-marked bears, a correction to include subadult males and data on growth rate of the population to calculate an individual density index as in the southern study area (Zedrosser et al., in press).

Multilocus heterozygosity

Tissue samples were collected from all bears immobilized. Eighteen microsatellite primers, described in Paetkau & 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 analyses

In addition to the variables presented in the Introduction, we controlled for the effect of study area in the analyses because the study areas were 600 km apart and brown bears in the northern study inhabit a less productive and mountainous area and occur at generally lower population densities. In relation to the carrying capacity in the two study areas, which is higher in the southern area because of the less harsh environment, the population densities could be regarded as similar in the two study areas. For these reasons, we included a cohort × study area interaction and a study area × population density interaction in the statistical analyses.

Because we wanted to examine the relationship between body mass and several categorical and covariate factors, as well as control for the variation within individual females (several females produced more than one litter during the study), we used linear mixed models (LME) with maternal identity as a random variable in our analyses. In general, we expected linear relationships between the independent variables and the dependent variables. However, we expected a nonlinear relationship between maternal age and yearling size and mass, as suggested by the results of Derocher & Stirling (1998a), and a nonlinear relationship between

population density and yearling size and mass. For this reason we included second-order terms of these predictor variables. For the variable cohort we used deviation contrast coding (www.ats.ucla.edu./stat/splus/library/contrast_coding.htm) to investigate which cohort(s) differed from the overall mean.

To select the most appropriate model from a set of candidate models based on the predicted relationships, we used Akaike's information criterion (AIC_c, Burnham & Anderson, 1998), corrected for small sample sizes, which is based on the principle of parsimony. The model with the lowest AIC_c is considered to be the one explaining most of the variation by using the fewest parameters, but models with $\Delta AIC_c < 2$ should receive consideration in making inferences (Burnham & Anderson, 1998). The within-litter variation in size and mass of yearlings was analysed with paired t-tests. Two-tailed tests were used, and an α level of 0.05 was selected for statistical significance. S PLUS v. 6.2 (Insightful Corp., Seattle, WA, USA) was used in all statistical analyses. Mean values are presented with standard errors (SE).

Mortality of cubs-of-the-year was higher in the south than in the north, but in both areas most of the mortality took place during the mating season in May–June (Swenson *et al.*, 1997, 2001*b*), before the lactation peak during summer (Farley & Robbins, 1995). For this reason statistical analyses were carried out twice, using litter size in both spring (yearlings counted after the family group leaves the den) and fall (cubs-of-the-year counted before the family group enters the den). When unmarked females with yearlings were captured, the number of yearlings present was assumed to reflect the number of cubs-of-the-year present the previous fall. This was a reasonable assumption, because no winter mortality has been recorded for cubs-of-the-year during their second winter (J. E. Swenson *et al.*, unpubl. data).

Results

We obtained body measurements from 226 yearlings (64 females and 69 males in the south and 47 females and 46 males in the north) during 1989–2002 (Table 2). Yearling mass ranged from 8 to 48 kg ($\bar{X} = 24.5 \pm 0.5$), and head

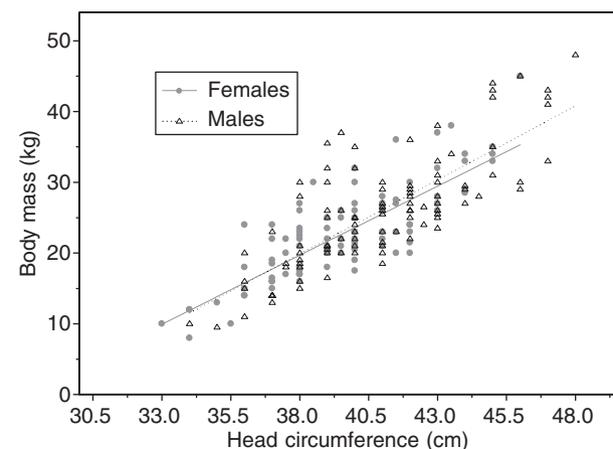**Table 2** Mean head circumference (cm) and body mass (kg) of brown bear yearlings *Ursus arctos* in Sweden

Litter size	Sex	Head circumference (cm)	Body mass (kg)	*n*
One	Males	42.6 ± 1.6	36.0 ± 3.6	6
	Females	42.3 ± 1.0	29.3 ± 3.5	7
Two	Males	41.9 ± 0.5	28.3 ± 1.2	47
	Females	40.0 ± 0.4	23.5 ± 0.9	41
Three	Males	40.1 ± 0.3	23.5 ± 0.7	57
	Females	39.3 ± 0.3	22.1 ± 0.7	60
Four	Males	38.8 ± 1.3	19.1 ± 3.7	5
	Females	36.5 ± 0.8	17.2 ± 3.9	3

Litter size is the number of cubs-of-the-year in the previous fall. Means are presented with ± 1 SE.

circumference varied from 33 to 48 cm ($\bar{X} = 40.3 \pm 0.2$). There was a significant linear relationship between body mass and body size of yearling brown bears [β(slope) $= 2.057 \pm 0.101$, $t = 20.304$, $n = 224$, $P < 0.001$, $R^2 = 0.647$; Fig. 1] and the slope of the regression lines did not differ between the sexes ($F = 0.341$, d.f. $= 1$, $P = 0.564$).

Yearling body size and mass were positively related to maternal size (Tables 1, 3 and 4). Maternal age apparently did not have a strong influence on yearling size or mass (Table 1). Positive relationships of yearling size and mass with maternal age were suggested in two of the candidate models (size: $\beta = 1.988 \pm 1.025$, d.f. $= 145$, $t = 1.940$, $P = 0.054$; mass: $\beta = 4.882 \pm 2.096$, d.f. $= 143$, $t = 2.329$, $P = 0.021$), which decreased in strength with increasing maternal size (size: $\beta = -0.033 \pm 0.017$, d.f. $= 145$, $t = -1.970$, $P = 0.051$; mass: $\beta = -0.083 \pm 0.034$, d.f. $= 143$, $t = -2.417$, $P = 0.017$); however, these models had ΔAIC_c values of 10.3 and 3.8 for yearling size and mass, respectively. Models including the second-order term of maternal age (suggesting nonlinear relationships between maternal age and yearling size and mass) had ΔAIC_c values of 3.1 and 6.0 for size and mass, respectively.

Body size and mass of yearling brown bears were negatively related to litter size (Tables 1, 3 and 4). The model including litter size in spring and the model including litter size in fall were quite similar, but the latter gave a somewhat better explanation of the variance. We obtained body measurements from all littermates in 40 twin and 37 triplet litters for analysis of within-litter variation. For simplicity we focused on body mass only, but using body size gave similar results. In twins, the heaviest yearling ($\bar{X} = 27.9 \pm 1.2$ kg) was on average 2.8 ± 0.4 kg heavier than the lightest yearling ($\bar{X} = 25.2 \pm 1.2$ kg, paired $t = 6.612$, d.f. $= 39$, $P < 0.001$). The average difference between the heaviest and lightest littermate in twins was not related to the sex ratio in the litter (male litter mates, $\bar{X} = 3.1 \pm 0.8$ kg, $n = 12$; female littermates, $\bar{X} = 1.9 \pm 1$ kg, $n = 10$; mixed sex, $\bar{X} = 3.0 \pm 0.5$ kg, $n = 18$, $F_{2,37} = 0.692$, $P = 0.514$). In triplet

Figure 1 Relationship between head circumference and body mass of male and female yearling brown bears *Ursus arctos* with the least-squares regression lines.

litters there was also variation in body mass within a litter [general linear model (GLM) repeated measurement, $F_{2,35} = 101.103$, $P < 0.001$]. The mean mass of the heaviest yearling was 25.9 ± 0.8 kg, the middle yearling 23.5 ± 0.8 kg and the lightest 20.3 ± 0.8 kg, all of which were different ($P < 0.001$). The average difference in body mass between the lightest and the heaviest littermate was larger in triplets than in twins (5.6 ± 0.5 kg or $29.5 \pm 2.8\%$ and 2.8 ± 0.4 kg or $12.2 \pm 2.2\%$, respectively, $t = 4.483$, d.f. $= 75$, $P < 0.001$; Table 1). Body mass of all littermates in quadruplets was only obtained in two litters, but the difference between the lightest and heaviest yearling was 5 and 12 kg or 50 and 67% in these litters.

Males were larger and heavier than females (Tables 1, 3 and 4). In twins of mixed sex, males were heavier than females by an average of 2.3 ± 0.7 kg (paired $t = 3.422$, d.f. $= 17$, $P = 0.003$). In 17 of 24 triplets of mixed sex, the heaviest yearling was a male, different from the expected 50:50 ($\chi^2 = 4.167$, $P = 0.041$).

Body size and mass were not related to multilocus heterozygosity ($F = 1.834$, d.f. $= 1$, $P = 0.179$ and $F = 0.394$, d.f. $= 1$, $P = 0.534$, respectively; Table 1). Body size and mass decreased with increasing population density (Tables 1, 3 and 4). There were indications of curvilinear relationships with population density, but the models including the second-order term of population density had ΔAIC_c values > 12 and 7 for body size and mass, respectively. However, there was more support for a stronger negative effect of population density on yearling mass in the southern study area than in the northern study area ($t = 2.021$, d.f. $= 144$, $P = 0.045$, $\Delta AIC_c = 0.424$).

Body size and mass of yearlings varied among cohorts, and did not co-vary in the two study areas (Tables 1, 3 and 4). Yearlings were heavier than average in 1990, 1991 and 1992, and lighter than average in 1996, 2000 and 2002. Yearlings were heavier in the north than in the south in 1991 and 1992, and heavier in the south than in the north in 1996, 1997, 1999, 2000 and 2002. Yearling size followed more or less the same cohort and cohort × study area interaction patterns as yearling mass. Yearling size and mass did not differ between the two study areas (Tables 3 and 4). Using maternal identity as a random variable revealed that the within-mother variation (SD $= 1.674$ and 3.263 for yearling size and mass, respectively) was almost as great as between-mother variation (SD $= 1.801$ and 4.670, respectively).

One hundred and twenty yearlings were tracked by radio-telemetry until the age of 3 years. Fourteen individuals died during this time period because of intraspecific predation ($n = 8$), unknown causes (not human induced, $n = 5$), and one was killed by a moose *Alces alces*. Survival increased with body size as a yearling ($\beta = 0.311 \pm 0.128$, $n = 120$, $P = 0.009$; Table 1), but body mass seemed to have a weaker effect on survival ($\beta = 0.089 \pm 0.055$, $P = 0.082$).

Discussion

Body size (head circumference) and mass in yearling brown bears were strongly correlated, and yearling body size and

mass were influenced by the same explanatory variables. Nevertheless, the relationships between body mass and maternal size and litter size were more statistically significant than the corresponding relationships between body size and maternal size and litter size.

As predicted (1), body size and mass of yearling brown bears were positively related to maternal size, which is consistent with the findings in many mammals (e.g. polar bears, Derocher & Stirling, 1998a; red deer *Cervus elaphus*, Clutton-Brock *et al.*, 1988; southern elephant seals

Table 3 Parameter estimates and test statistics for the analysis of body size (head circumference) of 226 brown bear yearlings *Ursus arctos* based on the model with the lowest AIC_c value

Explanatory variables	Parameter estimate	SE	t	P
Intercept	31.487	5.600	5.623	<0.001
Maternal size	0.188	0.090	2.088	0.039
Litter size	−0.527	0.285	−1.851	0.066
Sex (male vs. female)	1.039	0.264	3.941	<0.001
Population density	−0.055	0.021	−2.595	0.010
Cohort	[a]		5.854[b]	<0.001
Study area (south vs. north)	−0.007	0.764	−0.008	0.993
Cohort × study area	[a]		3.638[b]	<0.001

Explanatory variables used in the candidate models were maternal size, litter size (number of cubs-of-the-year in the previous fall), sex, genetic heterozygosity, population density, cohort and study area, and the interactions cohort × study area and study area × population density. Maternal identity was used as a random variable.
[a] Parameter estimates are not given due to the large number of estimates (see text).
[b] F statistics (type III).
AIC_c, Akaike's information criterion.

Table 4 Parameter estimates and test statistics for the analysis of body mass of 224 brown bear yearlings *Ursus arctos* based on the model with the lowest AIC_c value

Explanatory variables	Parameter estimate	SE	t	P
Intercept	−6.567	11.917	−0.551	0.582
Maternal size	0.670	0.191	3.500	<0.001
Litter size	−2.481	0.593	−4.181	<0.001
Sex (male vs. female)	1.902	0.526	3.614	<0.001
Population density	−0.130	0.048	−2.691	0.008
Cohort	[a]		8.132[b]	<0.001
Study area (south vs. north)	0.005	1.766	0.002	0.998
Cohort × study area	[a]		9.032[b]	<0.001

Explanatory variables used in the candidate models were maternal size, litter size (number of cubs-of-the-year in the previous fall), sex, genetic heterozygosity, population density, cohort and study area, and the interactions cohort × study area and study area × population density. Maternal identity was used as a random variable.
[a] Parameter estimates are not given due to the large number of estimates (see text).
[b] F statistics (type III).
AIC_c, Akaike's information criterion.

Mirounga leonina, Arnbom *et al.*, 1997; roe deer, Andersen *et al.*, 2000).

Surprisingly, the predicted relationship (2) between maternal age and offspring size was weak (judged from the high ΔAIC_c values of models including this term). The most likely explanation is that our sample included only five females older than 14 years, the age at which offspring size started to decrease in polar bears (Derocher & Stirling, 1994, 1998*a*). It might also be that maternal age in brown bears affects other reproductive variables, such as litter size, as reported for polar bears (Derocher & Stirling, 1994), more strongly than offspring size *per se*.

Body size and mass decreased with increasing litter size as predicted (3), which is consistent with the trade-off between number and size of offspring (Smith & Fretwell, 1974; Lloyd, 1987) that has been reported in several species (e.g. Foltz, Hoogland & Koscielny, 1988; Allaine *et al.*, 1998; Derocher & Stirling, 1998*a*). Also as predicted (4), within-litter variance in offspring body mass increased with litter size. Derocher & Stirling (1998*a*) reported the same pattern in polar bear cubs-of-the-year, and suggested that this was a result of increasing competition for limited maternal resources (milk), and because mothers might be constrained in their ability to control the variation in offspring size (McGinley, Temme & Geber, 1987). Thus, the competitive ability of individual cubs-of-the-year may be more important in large litters than in small litters.

As predicted (5), we found that males were on average larger and heavier than females among litters, and analyses of within-litter variation revealed that in a litter of mixed sex the heaviest yearling usually was a male. This result is consistent with the idea that mothers invest more in males than in females in sexually dimorphic polygynous species (Maynard-Smith, 1980). A size difference at yearling age, however, does not need to be a result of sex-biased maternal investment. First, milk transfer might not be under maternal control, but more dependent on sibling competition (Mock & Parker, 1997); second, size and mass at yearling age might be more a result of sex-biased feeding patterns of solid food [as indicated for bison *Bison bison* (Wolff, 1988) and white-tailed deer *Odocoileus virginianus* (Verme, 1989)] than sex-biased maternal expenditure, because cubs-of-the-year start to feed on solid food during their first summer. However, no measurements of milk transfer were available to test whether mothers invested more in their male offspring. Further, as the sexual size and mass differences recorded in yearling brown bears were small, questions arise as to their significance in terms of total maternal investment. Derocher & Stirling (1998*a*) argued that biased maternal investment in male polar bear cubs might be unlikely, because juvenile mortality seemed to be dependent on juvenile size (Derocher, Andriashek & Arnould, 1993; Derocher & Stirling, 1996), and investing disproportionally in males could increase mortality of female cubs. Survival of subadult (1–3 years old) brown bears was positively related to yearling body size as predicted (9), whereas mortality in brown bear cubs-of-the-year seem to be more related to social factors (sexually selected infanticide) than environmental

conditions (Swenson *et al.*, 1997, 2001*b*; A. Zedrosser *et al.*, unpubl. data). Thus, to the extent that maternal investment in different sexes is under maternal control, mothers should balance male-biased investment against the survival of female offspring. Although males are larger and heavier than females as yearlings, sexual size dimorphism in adult bears might be more an effect of extended periods of growth in males compared with females (Kingsley, Nagy & Reynolds, 1988; Derocher & Wiig, 2002; Derocher, Andersen & Wiig, 2005).

Contrary to our prediction (6) multilocus heterozygosity had no influence on yearling size or mass. Several studies have evaluated potential relationships between multilocus heterozygosity and fitness-related traits in vertebrates with various results. In mammals, studies of e.g. harbor seals *Phoca vitulina* (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. However, Zedrosser *et al.* (in press) reported that size of adult female brown bears was not related to multilocus heterozygosity; therefore, multilocus heterozygosity does not seem to influence body size in brown bears at any age. Similarly, Curik *et al.* (2003) found no large overall effects of microsatellite heterozygosity on 27 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).

If food abundance was similar throughout the entire study area, we would expect that individuals in areas with higher population densities should have been smaller and lighter than those living at lower densities (prediction 7) because the per capita food abundance should decrease with increasing population density (Welch *et al.*, 1997). We found that size and mass of yearling brown bears decreased with increasing population density as did Zedrosser *et al.* (in press) for size of adult female brown bears, which has previously not been demonstrated clearly in any bear species. As also found for adult females, our results suggest that the negative effect of population density on yearling size and mass was strongest in the southern study area. Our results support the physiological constraint hypothesis (e.g. Stearns, 1992): brown bears were smaller at high densities because their growth was limited by resource availability. Density-dependent body mass relationships have been reported for several species [e.g. Hjeljord & Histøl (1999) for moose; Macdonald *et al.* (2002) for badgers *Meles meles*]. On the contrary, Andersen & Linnell (1997) reported that a fourfold increase in population density did not affect postnatal growth rates in roe deer. Although the population density was generally higher in the southern study area, body size and mass overall did not differ between the study areas. From the negative effect of population density alone, one should expect yearling brown bears to be smaller in the south than in the north. However, the northern study area is less productive and the carrying capacity is probably

considerably lower than in the southern study area. Zedrosser *et al.* (in press) even found that adult female brown bears were larger in the southern study area, which demonstrates the difference in environmental conditions in the two study areas.

The cohort effect in yearling body size and mass (prediction 8) was probably related to different food availability among years (Nilsen, 2002). Rogers (1976) reported that predenning black bear cubs-of-the-year were on average 40% heavier in years with abundant food than in years of scarcity. Brown bears, which are typical capital breeders, largely rely on stored adipose tissue for reproduction. Thus, early maternal expenditure is dependent on the food availability during summer and especially the fall, when pregnant females add adipose tissue and muscles to meet their own metabolic needs, as well as the energetic costs associated with gestation and lactation during hibernation. Food availability during the year cubs-of-the-year are born influences lactation during summer and fall as well as the offsprings' own feeding on solid food. For this reason it is likely that abundant food in two consecutive years will result in a cohort with large and heavy yearlings. Food availability is likely influenced by climatic conditions, but how this influences the various food resources important for bears (moose, semi-domestic reindeer *Rangifer tarandus*, ants *Formica* spp. and *Camponotus* spp., grasses and forbs, and berries *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum*; Dahle *et al.*, 1998; Persson *et al.*, 2001) is complex and cannot be evaluated here. Reported cohort variation in body mass is often related to population density [e.g. Pettorelli *et al.* (2002) in roe deer; Solberg *et al.* (2004) in moose], and the effects of population density experienced as young can be transferred into adult age (Pettorelli *et al.*, 2002; Solberg *et al.*, 2004). Like Solberg *et al.* (2004) we report a cohort effect on body size and mass in addition to the effect of population density on body size and mass.

Whether the individual variation in size and mass is transferred into adult age depends on the extent of compensatory growth of small/light individuals. Compensatory growth seems to vary among species (Allaine *et al.*, 1998; Sikes, 1998) and between sexes (Atkinson, Stirling & Ramsay, 1996; Toïgo, Gaillard & Michallet, 1999; Solberg *et al.*, 2004). Female brown bears seem to exhibit compensatory growth, as size in adults was not related to yearling size (Zedrosser *et al.*, in press).

Dahle & Swenson (2003a) analysed length of maternal care in relation to offspring size and litter size in the northern study population and found that the probability that mothers cared for offspring for an additional year beyond the yearling age increased with decreasing body mass of yearlings. They speculated that yearlings were almost always weaned in the southern study area because yearlings might be heavier in more southern populations. However, as we did not find any difference in size or mass between the two study areas, size or mass of yearlings *per se* is not able to explain the difference in length of maternal care in the two populations.

We have demonstrated that size and mass of yearling brown bears are influenced by a number of factors. Heavier offspring are often reported to survive better than light ones in several species, e.g. red deer (Albon *et al.*, 1987), bighorn sheep *Ovis canadensis* (Festa-Bianchet *et al.*, 1997) and polar bears (Ramsay & Stirling, 1988; Derocher & Stirling, 1996). Although we measured offspring size and mass as yearlings, we assume that their size reflects their size and mass as cubs-of-the-year in the previous fall. In our study populations the major cause of mortality of cubs-of-the-year seemed to be infanticide by males (Swenson *et al.*, 1997, 2001b). Interestingly, survival of cubs-of-the-year seemed to increase with litter size, probably because females defended large litters more than small litters (A. Zedrosser *et al.*, unpubl. data). Because offspring size decreased with litter size, the relationship between offspring size and survival might be complex and different among populations. As predicted (9), survival from the age of 1–3 years increased with increasing yearling size. Similarly, Rogers (1976) reported that lightweight American yearling black bears *U. americanus* had lowered survival. Intraspecific predation is a major cause of natural mortality among subadults (Swenson *et al.*, 2001a). Perhaps small subadults are easier to capture and kill than larger ones.

We conclude that maternal size positively affects size and mass of yearlings and that yearling size and mass were negatively related to litter size. Yearling males were larger and heavier than females, similar to findings in most sexually dimorphic polygynous species. Body size and mass of yearlings decreased with increasing population density and varied significantly among cohorts. Survival of subadult brown bears increased with increasing body size and mass.

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