

LIFE-HISTORY STRATEGIES OF BROWN BEARS

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PhD thesis

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“Descended from the apes! My dear, let us hope that is not true, but if it is, let us pray that it will not become generally known.” – The wife of the bishop of Worcester after she heard about Charles Darwin’s “The Origin of Species”.

"Evolution is a *theory*', just like gravity. If you don't like it, go jump off a bridge." –
Anonymous

Abstract

This thesis deals with several life history aspects of the brown bear *Ursus arctos*. An organism's life-history is its lifetime pattern of growth, reproduction and mortality. It is formed by a long-term evolutionary process, but may also result from an immediate response of an organism to the environment to which it is exposed.

We found that yearling body size and mass were positively related to maternal size, and negatively related to litter size and population density. Yearling males were larger and heavier than females. Yearling body size and mass varied among cohorts, probably a result of fluctuating food conditions. Survival of subadult brown bears from age 1 to 3 increased with increasing yearling body size.

Scandinavian female brown bears reached 90% of their asymptotic size at 4.1-4.7 years. Individual body size variation of female brown bears was negatively related to density-dependent factors and positively correlated to density-independent fluctuations in the environment. Density-dependent factors may operate by increasing competition for food, resulting in a decrease in body size. Yearling body size was not important in explaining adult size, because initially smaller individuals showed compensatory growth when experiencing good food conditions.

We studied male annual reproductive success (ARS) and its determinants by using molecular techniques to determine paternity. In general, older and larger males had higher ARS. This may be due to advantages they have in a male dominance hierarchy, male-male competition and in endurance competition. Male ARS was positively correlated with population density, which may be related to the structure of an expanding bear population, with relative female densities declining towards the population edge. Internal relatedness, a measure of genetic heterozygosity, was negatively correlated with ARS, suggesting that outbred individuals have a higher ARS.

We investigated different factors possibly influencing mate selection of female brown bears in relation to the sexually selected infanticide hypothesis (SSI). Among males available in the vicinity of the females, the geographically closest, most heterozygous and less inbred, and largest males were more often the fathers of the female's next litter. Female brown bears may select the closest males as a counterstrategy to SSI and may exercise postcopulatory cryptic choice, based on physical attributes, such as a large body size, that reflects male genetic quality.

We evaluated the fitness benefits of two proposed reproductive strategies, abandonment of single cubs and reduced maternal defense of small litters. We modeled whether it might be a selective advantage for mothers to abandon single cubs. The advantage of abandoning singletons was negligible (0.04%) for females with a 2-year reproductive cycle, and small (0.97%) for females with a 3-year reproductive cycle. In the study area where SSI was a major agent of cub mortality, the probability of losing cubs decreased with increasing litter size. Our results support the maternal investment theory, because the litter-size related willingness to defend offspring against infanticidal males was the most deciding factor for cub loss. We did not find relationships between cub loss and environmental conditions and maternal age.

Primiparous females had significantly smaller litters and smaller yearling offspring than multiparous females. An analysis of the probability of cub loss of primiparous mothers showed that this probability increased with male turnover (a variable identifying SSI), but was not related to environmental conditions, body size of the mother or population density. We suggest that primiparous mothers are less able to or less experienced in defending their offspring against SSI.

Females that dispersed outside their mother's home range reproduced earlier than philopatric females. Brown bear females form matrilinear assemblages with related females using a common and largely exclusive area. Behavioral reproductive suppression might develop due to a hierarchical system among females within a matrilinear assemblage or due to inbreeding avoidance, because male brown bears can overlap with their daughters. Due to the low risk of inbreeding and frequent exposure of young females to unrelated males, we conclude that resource competition within female hierarchies causes reproductive suppression in young females.

We documented an apparent case of human-induced life-history change in brown bears. As predicted by life-history theory, populations with a long history (>50 generations) of human persecution showed a greater reproductive investment relative to body mass than populations with a short history (<15 generations). Also, female Scandinavian brown bears reproduce earlier in relation to their size and body mass than North American females. As a result, populations with a long history of exploitation are the world's most productive, which may explain why many of these populations have responded more positively to changes in management in recent times than most populations in North America.

List of papers

Body size, mass and growth

Paper I

Dahle, B., Zedrosser, A., Swenson, J.E. 2006. Correlates with body size and mass in yearling brown bears. *Journal of Zoology* (in press).

Paper II

Zedrosser, A., Dahle, B., Swenson, J.E. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* (in press).

Mate choice and male reproductive success

Paper III

Bellemain, E., Zedrosser, A., Manel, S., Waits, L.P., Swenson, J.E., Taberlet, P. 2006. The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide. *Proceedings of the Royal Society B* 273: 283-291.

Paper IV

Zedrosser, A., Bellemain, E., Taberlet, P., Swenson, J.E. Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. Submitted.

Female reproductive patterns and strategies

Paper V

Zedrosser, A., Dahle, B., Vik, J.O., Swenson, J.E. Offspring abandonment and maternal defense as reproductive strategies in brown bears. (2nd revision submitted).

Paper VI

Zedrosser, A., Dahle, B., Støen, O.G., Swenson, J.E. Primiparity, litter size and cub survival in a species with sexually selected infanticide, the brown bear. Submitted.

Paper VII

Støen, O.G., Zedrosser, A., Wegge, P., Swenson, J.E. Socially induced delayed primiparity in brown bears *Ursus arctos*. Behavioral Ecology and Sociobiology (in press).

Human-induced life-history patterns

Paper VIII

Swenson, J.E., Zedrosser, A., Gossow, H. Human induced life-history changes promote conservation of brown bears. Manuscript.

Introduction

“Why study life histories? Life histories lie at the heart of biology; no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and the complexities of their life cycles. Fascinating in themselves, life histories are also the keys to understanding related fields. Life-history theory is needed to understand the action of natural selection, a central element of evolution, the only theory that makes sense in all of biology. It also helps us understand how the other central element, genetic variation, will be expressed. The evolution of life-history traits and their plasticities determines the population dynamics of interacting species. Its explanatory power, barely tapped, could reach as far as communities. There is much to be done.”

S. C. Stearns, 1992, *The Evolution of Life Histories*.

An organism's life-history is its lifetime pattern of growth, reproduction and mortality, formed by a long-term evolutionary process, but may also result from an immediate response of an organism to the environment to which it is exposed (Begon et al. 1990). Life-history theory deals directly with natural selection, fitness, adaptation, and constraint, and is needed to understand the action of natural selection and how genetic variation is expressed (Stearns 1992). Empirical tests of theories in life-history evolution in large mammals (> 10kg) are rare, because they require long-term individual-based data, such as body mass, growth pattern, age at maturity, size at maturity, or number, size, and sex ratio of offspring. A certain trade-off, to speak in life-history terms, exists in projects compiling long-term data necessary for life-history studies. On the one hand these projects are very expensive and difficult to carry out; large mammals usually occur at low densities, are long-lived, are difficult to follow over a long time, and every individual shows a difference in its personal life-history. But on the other hand, the few studies carried out have contributed significantly to our knowledge and understanding of life-history theory, evolution and biology itself. The major life-history studies in large mammals have been carried out on ungulates (e.g. Clutton-Brock et al. 1980, 1982, Festa-Bianchet et al. 1995, 1998, 2000); however despite the large research and conservation interest in large carnivores, there is little research and information on their life histories. Below I give

a short introduction to the model species and the major life-history topics of this thesis.

The model species

This thesis uses the brown bear (*Ursus arctos*) as a model species to answer questions about life-history aspects of large mammals, especially of large carnivores. The brown bear is the most widely distributed of the eight bear species (Servheen et al. 1999, Schwartz et al. 2003a). It occupies habitats ranging from dense forests, subalpine and alpine mountain areas, to deserts and tundra (Servheen et al. 1990). The former and current distribution of the brown bear covers large parts of the northern hemisphere in Europe, Asia and North America. Human persecution has caused its range to shrink, and nowadays in Europe, large and viable populations are only found in eastern and northern Europe, whereas the populations in south-central and southwestern Europe are small, isolated, and probably not viable (Swenson et al. 2000, Zedrosser et al. 2001). Because especially the Alpine and Pyrenean populations were reduced to very few individuals (Swenson et al. 2000), reintroduction and augmentation programs were or are currently carried out, although the success of these conservation measures is uncertain (Zedrosser et al. 2001).

Brown bears are sexually dimorphic, with males about 1.2-2.2 times larger than females (Schwartz et al. 2003a), and have a multi-year growth pattern. Differences in body size and mass between males and females are influenced by population, age of the individual, season of sampling, and reproductive status. Adult bears in this study usually weighed between 80-110 kg (females) and 180-220 kg (males) in spring. The species exhibits up to 7 months of winter dormancy (hibernation) without eating, drinking, defecating, or urinating (Craighead et al. 1976, Schwartz et al. 2003a). Prior to hibernation, brown bears add 20-40% of their spring body weight in fat for the time of dormancy. Amounts of fat loss during hibernation are influenced by the previous seasons' food conditions, length of hibernation, sex and reproductive status.

McLellan (2005) has described the mating system of brown bears as a scramble competition polygamous mating system, however the large sexual size dimorphism, intense physical competition among males for the access to females in estrous (Schwartz et al. 2003a), and the skewed male reproductive success (Craighead et al. 1995b, paper III) also point out the importance of contest competition. During the

mating season in mid-May to early July (Dahle and Swenson 2003), a male may mate with several females and a female may mate with several males (Craighead et al. 1995b, Schwartz et al. 2003a, paper III, paper IV). Females may have a litter with offspring sired by different males (Craighead et al. 1995b, paper IV). The earliest recorded age of primiparity in brown bears is 3 years (Zedrosser et al. 2004), whereas the mean age of primiparity was 4.5 and 5.4 years in two populations in Scandinavia (Swenson et al. 2001). The average age of primiparity in the North American brown/grizzly bear is 6.6 years for interior and 6.4 years for coastal populations (McLellan 1994). Female bears are induced ovulators, i.e. eggs are released after behavioral, hormonal or physical stimulation, and may have 2 estrous periods of approximately 10 days (Craighead et al. 1995a, Boone et al. 1998). Implantation is delayed until November (Renfree and Calaby 1981, Tsubota et al. 1989), and the cubs are born during hibernation in January to March (Pasitschniak-Arts 1993, Schwartz et al. 2003a). Litter sizes range from 1 to 4 cubs, and only females care for the offspring, which follow their mother for 1.4-3.5 years (McLellan 1994, Schwartz et al. 2003a). Females do not mate until their offspring are weaned, which results in long and variable interbirth intervals. Longevity in the wild is 25 to 30 years, and reproductive senescence in females occurs around 27 years (Schwartz et al. 2003b).

Questions asked and related theories

Body size, mass and growth

Body size, mass and growth are important life-history traits, influencing behavioral, anatomical and physiological characteristics of an organism. Size or mass at birth or weaning is usually positively associated with early survival (Winters et al. 1947, Baker and Fowler 1992, Festa-Bianchet et al. 1997), and even with survival to adulthood (e.g.: Albon et al. 1987). Additionally, mass and size at birth or weaning is reported to correlate positively with body mass later in life (Schultz and Johnson 1995, Birgersson and Ekvall 1997), size as adults (Albon et al. 1987, Festa-Bianchet et al. 2000), and lifetime reproductive success (Festa-Bianchet et al. 2000, Steinheim et al. 2002). Larger and faster-growing individuals often reproduce earlier in life,

produce more offspring, produce offspring of better quality, and avoid predation better than small females (Stearns 1992).

The determinants of offspring and adult body size and how body size early in life affects survival, growth, age at maturity, adult size and reproductive performance is poorly understood in large carnivores, including brown bears. In papers I and II we investigated body size, mass and growth patterns of yearling and adult female brown bears in relation to sex, maternal attributes (size, age), litter size, environmental conditions, population density and multilocus heterozygosity. A short introduction to the mentioned variables is given below.

When evaluating the determinants of size and mass of yearling brown bears (paper I), sex is most likely an important factor. 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, which in polygynous species usually is the male (Trivers 1972, Maynard-Smith 1980). Adult male brown bears are on average twice as heavy as females and body size and mass positively affect male mating success (paper V, VI), as is reported for other polygynous species (e.g. McElligott et al. 2001). However, we acknowledge that there are competing hypotheses to explain why male yearlings should be larger and heavier than females at this age.

Male reproductive success in polygynous, size-dimorphic species is dependent on body size (Andersson 1994), and males probably have been selected to maximize growth rate (Clutton-Brock et al. 1988). In contrast, females in size-dimorphic species have to trade growth for reproduction and cannot grow as fast; several studies have suggested different growth patterns between males and females in ungulates (e.g.: Festa-Bianchet et al. 1994, LeBlanc et al. 2001, Toïgo et al. 1999). Brown bears exhibit a polygynous mating system and strong sexual size dimorphism (Schwartz et al. 2003a). We therefore restricted our analysis on the determinants of adult size (paper II) to female brown bears only.

Maternal body size may be an important factor influencing offspring body size, because larger females may produce larger and heavier offspring (Myers and Master 1983, Clutton-Brock et al. 1988, Wauters et al. 1993, Arnbohm et al. 1997). Offspring of larger mothers may also show increased pre-weaning growth (Myers and Master 1983, Arnbohm et al. 1997, Barbraud et al. 1999). Body size and age are often correlated in mammals, and 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 and Gaillard 2001). Derocher and Stirling (1994, 1998) found that litter mass, litter size and offspring size were related to maternal age in polar bears (*Ursus maritimus*). Therefore we evaluated the effects of maternal size and age on yearling body size and mass in paper I.

Life-history theory predicts a compromise between the number and size of offspring (Smith and Fretwell 1974), and such a negative relationship has been reported in a wide variety of taxa (see Lloyd 1987 and Roff 1992 for reviews). In ungulates, Gaillard et al. (1998) reported that variation in growth within litters increased with litter size in roe deer (*Capreolus capreolus*). In polar bears, Derocher and Stirling (1998) found that the difference in body mass between siblings in triplet litters was approximately 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. Therefore we evaluated the effects litter size on yearling body size and mass in paper I.

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

Changing food conditions due to density independent environmental fluctuations have also been reported to influence body size in ungulates (e.g.: Solberg et al. 2004). Food availability differs among years and thus affects growth patterns of subadult individuals and ultimately their adult size. In ungulates, cohort effects on life-history parameters have been found repeatedly (e.g. Albon et al. 1987, Skogland 1990, Post et al. 1997), and size as adult is often positively correlated with body mass at birth or weaning (Albon et al. 1987, Festa-Bianchet et al. 2000). We controlled for cohort effects on yearling body size and mass in paper I, and for the effect of environmental conditions on adult female body size in paper II.

Surrogates for individual fitness have been reported to correlate with multilocus heterozygosity, however the interpretation remains controversial (Britten 1996). Significant multilocus heterozygosity-fitness correlations have been found in birds (e.g. Hansson et al. 2001) and mammals (e.g. Coltman et al. 1998, Slate et al. 2000). For example, Coltman et al. (1998) examined the relationship between fitness-related traits and microsatellite heterozygosity in wild harbor seal pups (*Phoca vitula*) and found that birth mass was positively influenced by individual heterozygosity. We evaluated the potential effect of multilocus heterozygosity on both yearling size and mass (paper I) and adult female size (paper II).

Patterns of mate choice and male reproductive success

Understanding the mechanisms that influence the reproductive success of individuals is essential to understand the mechanisms under natural selection. Analyzing the factors related to individual variation in reproductive success, and identifying the characteristics of successful individuals, gives insight into the selective pressures affecting evolutionary processes, especially if summed over a lifetime.

In mammals, males and females often use very different reproductive strategies. Due to the absence of paternal care in most mammals, male reproductive success is constrained only by the ability to sire offspring (Trivers 1972). Thus, male mammals usually compete intensely for mates, creating the potential for a high variance in male mating success (Emlen and Oring 1977), and thus an opportunity for sexual selection (Wade and Arnold 1980, Arnold and Wade 1984). Sexual selection, however, can only occur if variation in mating success is correlated with phenotypic variation (Andersson 1994). Sexual dimorphism and weaponry have most likely evolved as adaptations in species in which males compete for access to females (Andersson 1994).

Bears are sexually dimorphic species, and male mating success is strongly influenced by fighting for access to females. Females are usually the more selective sex in mate selection, because of the higher reproductive investment of females than males (Darwin 1871, Clutton-Brock 1989). Females may gain direct benefits (increased fecundity or amelioration of a cost) and/or indirect benefits (increased fitness of their offspring) by choosing a high-quality reproductive partner (e.g. Kokko et al. 2003). However, female choice is rarely obvious and can even be very subtle or

cryptic, occurring during or even after mating (Birkhead and Møller 1993, Eberhardt 1996). Female choice may also be context-dependent. For example, female choice may differ for species in which young are vulnerable to sexually selected infanticide (SSI), i.e. where males kill dependent offspring, but not their own progeny, to gain access to breeding opportunities with the mother (Hrdy 1979). This phenomenon is rarely of benefit to females, and may lead to a dilemma: select a high-quality mating partner or prioritise mating strategies to counter infanticide. A potential counterstrategy to SSI is multiple mating, or “promiscuity”, in which the female attempts to confuse paternity. This idea has received much support in recent decades, and paternity uncertainty has been hypothesised as a major factor explaining multi-male mating by female mammals (Wolff and Macdonald 2004). In paper III we investigated the factors determining annual reproductive success in males, and in paper IV we investigated mate choice patterns of female brown bears. A short introduction to the factors influencing male reproductive success and female mate selection is given below.

Intrasexual selection favors traits that confer an advantage on males in gaining access to females (Andersson 1994). Morphological traits, such as body size, weaponry and intense signals of fighting ability, are essential in male-male competition and are also expected to be important cues in female choice (Andersson 1994). When male mating success is strongly influenced by fighting, sexual selection promotes sexual size dimorphism, with males larger than females. Therefore male reproductive success is then expected to be biased towards a few large adults with superior competitive abilities. Intersexual selection may also favor large male size, if females prefer large males (Andersson 1994). Body size has often been found to be a major contributing factor to male reproductive success (e.g. red deer, *Cervus elaphus*, Clutton-Brock et al. 1982, 1988).

Body size and age are closely linked in many large mammals, and also age is often associated with male reproductive success (e.g. Clutton-Brock et al. 1982, 1988). Older males are often more experienced (East et al. 2003) and more dominant (Clutton-Brock et al. 1988, LeBoeuf and Reiter 1988), and therefore superior competitors in male-male competition. As viability selection leads to older males of higher genotypic quality than younger males, females should theoretically prefer to mate with older males (Trivers 1972), provided that survival rates are not age-dependent (Beck and Powell 2000).

From a genetic perspective, superior reproductive competitors may have greater multilocus heterozygosity, which is often correlated with fitness-associated traits (David 1998, Hansson and Westerberg 2002). Also females may gain genetic benefits by selecting the most heterozygous males (Brown 1997). Females may base their choice on traits directly reflecting heterozygosity at key loci or at many loci, such as the expression of vigour, symmetry, or condition-sensitive ornaments. Finally, female mate selection is probably directed towards less related individuals as an efficient mechanism for inbreeding avoidance (Blouin and Blouin 1998).

Male reproductive success may also be influenced by population density, and mating skew may either increase or decrease with density (Kokko and Rankin 2006). On the other hand, female choice may be context-dependent as a mating strategy to counter SSI by paternity confusion.

Female reproductive patterns and strategies

Abandonment of dependent offspring has been documented in several species of birds and mammals (e.g. Fair 1978, Bustnes and Erikstad 1991, Fairbanks and McGuire 1995, Szekely and Cuthill 2000), and is most often viewed as detrimental to the mothers' fitness, because it reduces the number of offspring produced in a lifetime. Nevertheless, in species with a variable number of offspring, a mother may abandon dependent offspring as reproductive strategy. A mother could increase her expected number of recruits to the population by rejecting a single offspring, if she has the possibility to produce a second, larger litter within a short time (Tait 1980).

Reduction of maternal defense can have an effect similar to abandonment, if it results in mortality of offspring. A situation where reduced maternal care can be of importance exists when males seek mating opportunities through SSI. According to the parental investment theory, defense of offspring should be related to the reproductive value of the offspring (Maynard-Smith 1984). Experimental tests of this hypothesis in rodents have shown that defense of young by mothers increases with the number of offspring (Maestripieri and Alleva 1991, Koskela et al. 2000). In paper VI we extend the model proposed by Tait (1980), and reevaluate the fitness gain to a mother brown bear by abandoning a singleton cub prior to or during the mating season and by providing maternal defense against cub loss. We also compare the relative importance of these proposed behavioural strategies.

Primiparity, that is giving birth for the first time, is a key event in the life-history of all animals (Stearns 1992). Primiparous females usually wean fewer and smaller offspring than multiparous females (Clutton-Brock 1991, Festa-Bianchet et al. 1995). The trade-offs between future and current reproduction (Williams 1966) and between growth and reproduction (Festa-Bianchet et al. 1995, Millar 1975, Tuomi et al. 1983) are life-history concepts that provide a theoretical basis for the relative low performance of first-time breeders (Künkele 2000). In addition, primiparous females may be smaller, i.e. not yet fully grown, than multiparous females, and larger females often produce larger and heavier offspring (Arnbom et al. 1997, Clutton-Brock et al. 1988, Myers and Master 1983, Wauters et al. 1993), and larger offspring may have higher survival (paper I). Inexperience may also cause primiparous females to be energetically less efficient in offspring production than multiparous females (Künkele 2000, Lunn et al. 1994), resulting in a lower reproductive performance. In addition, first-time breeders may lack refined behavioral skills associated with foraging (Becker et al. 1998) and parental care (Wang and Novak 1994). Inexperience and lack of skills by the mother may be of special importance for defending offspring if males seek mating opportunities by killing dependent offspring that are not their own, i.e. sexually selected infanticide (SSI) (Hrady 1979). In paper VI we investigated if primiparity had an effect on litter size, offspring size and cub survival in the brown bear and analyze litter survival of primiparous females in relation to the SSI hypothesis.

Reproduction by young animals is suppressed by adults or dominant individuals in many group-living and cooperatively breeding mammals, leading to delayed primiparity and failed reproduction attempts in philopatric females (Wasser and Barash 1983, Creel and Creel 1991, Waterman 2002, Oli and Armitage 2003). Reproductive suppression can occur in subordinate females as a result of behavioral dominance by older females (reviewed by Wasser and Barash 1983) or when young females are not exposed to unrelated males (Wolff 1992, Lambin 1994). Such intrinsic reproductive suppression has been documented in several mammalian species, especially rodents and group-living carnivores (Wolff 1997). Brown bears are generally not considered to be territorial (Pasitschniak-Arts 1993, Schwartz et al. 2003a), but dominance hierarchies have been observed (Pulliainen et al. 1983), especially when bears aggregate at garbage dumps and at salmon (*Oncorhynchus* spp.) spawning streams (see IGBC 1987 for a review, Craighead et al. 1995a, Gende and

Quinn 2004). The distance between females decreases and the amount of overlap of their home ranges increases with increasing relatedness (Støen et al. 2005). This leads to the formation of matrilinear assemblages with related females using a common and largely exclusive area (Støen et al. 2005). Thus, although not gregarious, brown bears may be more social than previously assumed (Støen et al. 2005). A hierarchical system can develop within matrilinear assemblages and provide a possibility for reproductive suppression. In paper VII we investigated if dispersed females which are relieved from matrilinear and/or paternal influence would reproduce earlier than philopatric females.

Human-induced life-history patterns

Human-induced selection on species is likely not just a modern phenomenon. Although the current extinction crisis caused by human activities is unprecedented (Festa-Bianchet 2003), there is evidence that humans had a strong impact on species and species composition for several millennia (Kay 1994, Balmford 1996, Caughley and Gunn 1996). Human-induced selection due to harvesting is a potentially negative consequence of exploiting fish and wildlife populations. Its effect on life-history traits has been documented in commercially exploited fish populations (citations), but in large mammals, effects have primarily been documented regarding phenotypic traits, such as tusks on elephants (*Loxodonta africana*) (Jachmann et al. 1995) and horns on bighorn sheep (*Ovis canadensis*) (Coltman et al. 2003). In paper VIII we investigate an apparent case of human-induced life-history change in brown bears. We compared female brown bear reproductive investment in relation to body size and mass, and the relationship between mean female mass and mean litter size between populations with a long history (>50 generations) and a short history (<15 generations) of human persecution.

Objectives of the thesis

The main goals of the this thesis were to:

- 1) Evaluate which factors influence the body size of brown bears (paper I, II);

- 2) Evaluate the female mate choice and male reproductive success (paper III, IV);
- 3) Evaluate female reproductive patterns and strategies, also in relation so sexually selected infanticide (paper V, VI, VII);
- 4) Evaluate if humans potentially influenced the life history patterns of brown bears (paper VIII).

Methods and materials

Study areas and study populations

The study areas were in Dalarna and Gävleborg counties in south-central Sweden (approximately 61° N, 14° E, southern study area), and in Norbotten County, northern Sweden (approximately 67° N, 18° E, northern study area). Both areas are close to the northern and southern edges of the range of the Scandinavian brown bear population and are approximately 600 km apart.

The southern study area (south) consists of 13,000 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*), European aspen (*Populus tremula*) and gray alder (*Alnus incana*) are common. The elevations range from about 200 m in the southeastern part to about 1,000 m in the western part, but only a minority of the area is above timberline, which is about 750 m elev. Bears are intensively hunted in the entire area.

The northern study area (north) encompasses 8,000 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 2,000m. The valleys are dominated by mountain birch, Scots pine and Norway spruce. Mountain birch forms the tree line and occurs at a maximum elevation of 600 m (Grundsten 1997). Bears are protected in the national parks, but hunted in the surrounding areas. Both areas are further described in paper II.

Capture, handling and radio-telemetry

All bears in this study were captured as a part of a long-term project on brown bear ecology in Scandinavia (e.g.: Swenson et al. 1994, 1995, 2001a, b). Radiomarked female brown bears with yearling cubs were darted from a helicopter using a remote drug delivery system (Dan-Inject®). For ethical reasons we did not capture females with cubs-of-the-year. The standard capture procedure was to first immobilize the yearling offspring and then the mother. We used helicopters because it is the only method to continually recapture individuals. All captures were carried out in mid-April in the southern study area and in 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 body mass to immobilize the bears (Kreeger et al. 2002, Arnemo 2005). Atipamezol was used as an antidote for medetomidine (5 mg per 1 mg medetomidine) (Kreeger et al. 2002). A circular sample of surface tissue (diameter 6 mm) was taken for genetic analysis from an ear using a sterile dermal biopsy punch. For bears of unknown age, a first premolar was extracted for age determination (Matson et al. 1993).

We used VHF-radio-transmitters (Telonics®, model 500) for adult individuals. Yearling brown bears were not fitted with a radio-collar due to their fast growth pattern and to avoid having to recapture them every year to change the radio-collar. Instead a sterile peritoneal radiotransmitter (Telonics®, model IMP/400/L HC) was implanted in their peritoneal cavity following a standard biomedical protocol (Arnemo 2005). All capture and handling conformed to the current laws regulating the treatment of animals in Sweden and were approved by the appropriate Swedish ethical committee (Djuretiska nämnden i Uppsala). For further details regarding capture and handling of bears in our study refer to Kreeger et al. (2002), Arnemo (2005) and Arnemo et al. (2006). The bears were located weekly by telemetry using standard triangulation methods from the ground or from an aircraft (helicopter or fixed-wing) during their nondenning period (Dahle and Swenson 2003).

Genetic methods

All genetic samples were preserved in 95% alcohol until extraction. Eighteen microsatellite loci, described in Paetkau and Strobeck (1994) and Taberlet et al. (1997), were amplified using Polymerase Chain Reaction. The amplification and

analysis of microsatellites was carried out following the protocol described in Waits et al. (2000). Totally, our genetic database from bear tissue consisted of 977 genotypes (Bellemain 2004), including radio-marked and hunter-killed individuals. The probabilities of identity, i.e. the probability to obtain two identical genotypes, from two different individuals, by chance (PI , Paetkau and Strobeck 1994, PI_{sib} , for siblings Waits et al. 2001) were low ($PI = 3.10 \times 10^{-17}$ and $PI_{sib} = 3.10 \times 10^{-7}$) (Bellemain 2004).

For most of the offspring used in this analysis, the mother was known, because yearlings were captured while accompanying their mother. For bears with unknown pedigree, we determined parentage using the software PARENTE (Cercueil et al. 2003). Paternity probabilities were calculated using the same software, taking into account the allelic frequencies, global error rate and sampling rate of the population (Cercueil et al. 2003). One allelic incompatibility of 18 loci was allowed in the comparison of the father-offspring genotype in order to consider the 0.8% error rate in the genetic data set (Bonin et al. 2004).

Population density

An individual population density index was created to estimate differences in population density around a given individual. In the southern study area, a population size estimate, based on a DNA analysis of non-invasive sampling of scats, was carried out in 2001 and 2002 (Bellemain et al. 2005b). Following the procedures described in paper II we calculated an individual density index (within a radius of 17.84 km) around each radio marked individual in our analysis, which corresponds to the density of bears per 1000 km². The procedures used in paper II are based on the location of individuals genetically identified by the scat sampling, the location of the radiomarked bears (71% of the radio marked bears were represented in the genetic samples from scats (Bellemain et al. 2005b)), and the growth rate in the population (Sæther et al. 1998). This growth rate was used to temporally correct the density estimate throughout the study period.

In the northern study area virtually every adult male and female and all subadult female bears were radio-marked from 1995 to 2002 (Swenson et al. 2001). Following the procedures described in paper II we used these data and data on growth rate of the population (Sæther et al. 1998) to calculate an individual density index like in the southern study area. Although based on different methods, we regard the indices of

both study areas as comparable, because we are confident that virtually all individuals (except subadult males, which were accounted for) were radiomarked in the northern study area, and the density estimates based on the genetic sampling in the south was corrected by dividing it by the proportion of radiomarked bears identified in the genetic sample. The average population density index was 11.1 bears/1000km² in the north and 29.3 bears/1000km² in the south (Støen et al. 2006). See also paper II for further details.

Summary of results

Body size, mass and growth

Determinants of yearling body size (paper I)

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 were analyzed in relation to maternal size, litter size, sex, multilocus heterozygosity, population density and cohort. 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 3 offspring, where the heaviest yearling was on average 29.5 ± 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 age 1 to 3 increased with increasing yearling body size.

Determinants of adult female body size (paper II)

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

Mate choice and male reproductive success

Male annual reproductive success (paper III)

In this paper we studied male annual reproductive success (ARS) and its determinants (phenotypic characteristics, age, population density), using molecular techniques to determine paternity. We found a significant difference in male ARS between the study areas, with males producing fewer offspring annually in the south than in the north. In general, older and larger males had higher ARS. Older males may be more experienced in competition for reproduction (male dominance). Large body size is of direct benefit in male-male competition and of advantage in endurance competition for the access to females. Age was relatively more important for ARS in the north, and body size was more important in the south, which may be related to differences in male age structure in the study areas due to illegal killing. A single old male dominated the reproduction in the north during the study period, and this most likely resulted in the relatively higher importance of age in the north. In the south, the area with the more even male age structure, no single male was able to dominate. This most likely resulted in a more intense competition among males, with body size as the deciding factor. Male ARS was positively correlated with population density. This may be related to the structure of an expanding bear population, with female densities

declining towards the population edge. Internal relatedness, which is a measure of genetic heterozygosity, was negatively correlated with ARS, suggesting that outbred individuals have a higher ARS. Individual heterozygosity at key or many loci may be reflected in male physical qualities and condition-sensitive traits, and some of these traits may directly benefit males in contest or in sperm competition.

Female mate selection (paper IV)

In this paper we investigated different factors possibly influencing mate selection of female brown bears. We compared characteristics of males “chosen” to be fathers, as determined by genetic paternity tests, to those known to be available in the vicinity of the female. We assumed that SSI might influence female mate selection in brown bears, because females may apply mating counterstrategies to SSI. We hypothesize that females may be faced with a dilemma: either select a high-quality partner based on phenotypic criteria, as suggested by theories of mate choice, or rather mate with future potentially infanticidal males as a counter strategy to SSI. We evaluated which male characteristics were important in paternity assignment. Among males available in the vicinity of the females, the geographically closest, most heterozygous and less inbred and largest males were more often the fathers of the female’s next litter. We found evidence that female brown bears may select the closest males as a counter-strategy to infanticide and exercise a post-copulatory cryptic choice, based on physical attributes, such as a large body size, reflecting male genetic quality. However, male-male competition either in the form of fighting before copulation or during the post-copulatory phase, in the form of sperm competition, cannot entirely be ruled out.

Female reproductive success and strategies

Abandonment and maternal defense (paper V)

We evaluated the fitness benefits of two proposed reproductive strategies, reduced maternal defense of small litters and abandonment of single cubs, using data on cub mortality in brown bears in two study areas in Scandinavia. We found that singleton brown bear cubs had a higher mortality than cubs from larger litters. This can be explained by either abandonment to increase future reproduction or a lower defense of singletons by the mother in accordance with maternal investment theory. We modeled

the number of offspring that a female brown bear would recruit to the population, allowing them to vary their behavior regarding abandoning single cubs to evaluate if there might be a selective advantage to abandon single cubs. The advantage of abandoning singletons was negligible (0.04%) for females with a 2-year reproductive cycle, and small (0.97%) for females with a 3-year reproductive cycle. Hence, we rule out opportunistic abandonment as a major cause of cub loss. In the area where sexually selected infanticide (SSI) was identified as a major agent of cub mortality, the probability of losing cubs decreased with increasing litter size. Our results support the maternal investment theory, because the litter-size related willingness to defend offspring against infanticidal males was the most deciding factor for cub loss. We did not find relationships between cub loss and environmental conditions and maternal age. Protecting cubs from males is costly, because mothers with cubs tended to be killed more often by adult males than adult females without cubs.

Primiparity and its effect on reproduction (paper VI)

We studied the effects of primiparity on litter size, offspring size, and cub loss in brown bears in two study areas in Scandinavia. Sexually selected infanticide (SSI) has been previously suggested as a major mortality factor in one of the areas. We found that primiparous females had significantly smaller litters and smaller yearling offspring than multiparous females. The probability of cub loss for both primiparous and multiparous was significantly higher in the area where SSI was suggested (south), than in the area without SSI (north). A separate analysis of the south found suggestive evidence that primiparous females had a higher probability of cub loss than multiparous females. An analysis of the probability of cub loss of primiparous mothers showed that this probability increased with male turnover (a variable identifying SSI), but was not related to environmental conditions, body size of the mother or population density. In general, females in the south were primiparous earlier than females in the north, however females raised their first successful litter at the same age in both areas. We found suggestive evidence that females that were primiparous at age 4 in the south had the highest probability of cub loss. We suggest that primiparous mothers are less able to or experienced in defending their offspring against SSI.

Socially induced delayed primiparity (paper VII)

Reproductive suppression through behavioral or physiological means is common in group-living and cooperative breeding mammals, but to our knowledge it has not been shown in wild large carnivores other than those with a clear form of social organization. Brown bear females form matrilinear assemblages with related females using a common and largely exclusive area. Behavioral reproductive suppression might develop due to a hierarchical system among females within a matrilinear assemblage or due to inbreeding avoidance, because male brown bears can overlap with their daughters. We tested whether natal dispersal influenced age of primiparity. We predicted that emigrant females, geographically removed from maternal or paternal influence would reproduce earlier than philopatric females. The average age of primiparity was 4.3 years in females that dispersed outside their mother's home range and 5.2 years in philopatric females. Only overlap with mother's home range, and not body size, body mass, growth, local population density or overlap with father's home range had a significant influence on the age of primiparity. The ultimate role of reproductive suppression for brown bears is likely to avoid inbreeding or to minimize resource competition. Due to the low risk of inbreeding and frequent exposure of young females to unrelated males, we conclude that resource competition within female hierarchies causes reproductive suppression in young females.

Human-induced life-history patterns

Life-history differences between North America and Europe (paper VIII)

We documented an apparent case of human-induced life-history change in brown bears. As predicted by life-history theory, populations with a long history (>50 generations) of human persecution showed a greater reproductive investment relative to body mass than populations with a short history (<15 generations). Also, female Scandinavian brown bears reproduce earlier in relation to their size and body mass than North American females. As a result, populations with a long history of exploitation are the world's most productive, which probably explains why many of these populations have responded more positively to changes in management in recent times, than most populations in North America.

Discussion

Body size

Body size is an important factor for a brown bear throughout its life. Our results show that body size influences a brown bears survival as a yearling and subadult, that maternal size influences cub survival, and that body size influences a males' reproductive success and (paper I, II, III, IV, V, VIII).

Yearling body size is, amongst other factors, determined by maternal size (paper I), which is consistent with the findings in many mammals (e.g. polar bears, Derocher and Stirling 1998a; red deer, Clutton-Brock et al. 1988; southern elephant seals (*Mirounga leonine*), Arnbohm et al. 1997; roe deer, Andersen et al. 2000). However, to our knowledge we are the first to suggest that cub mortality due to SSI decreases with increasing maternal body size (paper V). Because brown bears are a solitary species, females do not form social coalitions to protect their offspring against SSI, as has been shown in socially living lions and primates (Packer and Pusey 1983, 1984, Sakamaki et al. 2001, Beehner et al. 2005). In species where females act in a group to counter infanticide, individual size may not be as important as in solitary species like bears. Because brown bears are a sexually dimorphic species (Schwartz et al. 2003a), differences in size and mass between males and females will be influenced by age, and old, large and experienced females may be able to better defend their cubs, especially against young, not yet fully grown males (McLellan 2005).

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; polar bears, Ramsay and Stirling 1988, Derocher and Stirling 1996). Because we do not capture brown bear cubs of the year for ethical reasons, we were not able to confirm this pattern for cubs. However, survival from the age of 1 to 3 years increased with increasing yearling size (paper I). Similarly, Rogers (1976) reported that lightweight American yearling black bears (*Ursus americanus*) had a lowered survival. Intraspecific predation is a major cause of natural mortality among subadults (Swenson et al. 2001a). We do not know the explanation for this high amount of intraspecific predation on yearlings, however given that this behavior occurs, perhaps small subadults are easier to capture and kill than larger ones.

The mating system of brown bears is based on male contest competition for females (Schwartz et al. 2003a), which is also indicated by the large sexual size dimorphism (Andersson 1994). Male body size was positively correlated with measures of reproductive success (paper III). This suggests that larger males are able to physically dominate and exclude smaller males when competing for estrous females, as has been found in several studies on other species (Clutton-Brock et al. 1988, LeBoeuf and Reiter 1988, McElligott et al. 2001, Wilson et al. 2002). In bighorn sheep, younger or subdominant males that were not able to tend an estrous female employed mating tactics like cursing and blocking relatively more often than adult males, which successfully tended estrous females (Hogg 1984). However, to our knowledge, no alternative mating tactics of younger or smaller males have been observed in brown bears. An alternative explanation for the importance of male body size may be that females more often select larger males (paper IV). Large body size in males could reflect their genetic quality and females may select their reproductive partner based on this criterion.

In paper II we found that females in the southern study area were larger than females in the north. This pattern is most likely explained by the shorter growing season and the lower primary productivity in the north. In addition, northern females hibernate for 6.9-7.9 months, depending on their reproductive status, whereas in the south females hibernate 5.3-6.9 months (Manchi and Swenson 2005). Thus southern females may be able to invest more energy into growth than in the fat accumulation necessary for hibernation. We were not able to confirm these different patterns of growth and body size between the study areas for males (paper III). Male reproductive success in polygynous, size-dimorphic species is dependent on body size (Andersson 1994), and males probably have been selected to maximize growth rate (Clutton-Brock et al. 1988). Several studies of ungulates have suggested different growth patterns between males and females (e.g.: Festa-Bianchet et al. 1994, LeBlanc et al. 2001, Toïgo et al. 1999). This lack of difference in male body size between the study areas, despite the environmental differences, may be related to sample size problems. In the south we had a number of individuals older than 10 years, even older than 20 years. In the north very few males were older than 10 years, and the only male older than 15 years was the largest individual ever to be captured in the course of our study. The lack of old males and this exceptionally large individual may have skewed the growth curve of males in the northern area.

Age

Brown bears have a multi-year growth pattern (Schwartz et al. 2003a), and some authors even suggest that they grow throughout their life (Kingsley et al. 1988). Not surprisingly, we found that body size is age dependent in bears (paper I, II, III). Male reproductive success was positively correlated with age and female brown bears seemed to preferably select old males (paper III, IV). We found no evidence of reproductive senescence in male brown bears, as occurs in male red deer (Clutton-Brock et al. 1988) and female brown bears (Schwartz et al. 2003b), because all males over 20 years reproduced regularly (paper III).

Females of many species choose to mate with old rather than young males, possibly because older males pass superior genes on to their offspring (Brooks and Kemp 2001). Age in males may reflect their genetic quality (Trivers 1972), and/or those males may also be more selected by females (Brown 1997). Older males may also show a higher reproductive effort, as in reindeer (*Rangifer tarandus*) (Mysterud et al. 2003), or they may be more experienced and efficient in the scramble competition for females.

Several studies show that male age is often strongly correlated with rank (Clutton-Brock et al. 1982, 1988, Le Boeuf and Reiter 1988, Coltman et al. 2001), however all of these studies dealt with species with temporary harem polygyny. Brown bears are considered to be a nonsocial species, however a spatial male dominance hierarchy based on age and size may exist, as suggested for brown bears at garbage dumps (Craighead et al. 1995a), and for American black bears (Kovach and Powell 2003) and polar bears (Derocher and Stirling 1990). Therefore selection of older males by females might also reflect selection of dominant males.

Age also influenced reproductive success patterns of females. We did not find a relationship between maternal age, cub loss and maternal defense of offspring (paper V), however, primiparous females lost more cubs than multiparous females and females primiparous at a younger age lost more cubs than females primiparous at an older age (paper VI). This seems contradictory, however in paper V we analyzed female age as a continuous variable, whereas in paper VI we specifically tested primiparous against multiparous females.

Derocher and Stirling (1994) reported a curvilinear relationship between maternal age and offspring body size in polar bears. We found this relationship to be weak in

brown bears (paper I). The most likely explanation for this result is that our sample included only 5 females older than 14 years, the age at which offspring size started to decrease in polar bears (Derocher and Stirling 1994, 1998). It might also be that maternal age in brown bears affects other reproductive variables, such as litter size, as reported for polar bears (Derocher and Stirling 1994), more strongly than offspring size per se.

Population density

We found that size and mass of yearling brown bears (paper I) and adult female size (paper II) decreased with increasing population density, which has previously not been demonstrated clearly in any bear species. 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 mammals (e.g. Skogland 1990, Hjeljord and Histøl 1999, Festa-Bianchet et al. 2000, Macdonald et al. 2002).

Overall population density appears to be related to food availability in bears (McLellan 1994), suggesting that food is the ultimate regulating factor. Density dependency may work by reducing the food base and/or increasing competition for food. In systems where food is highly concentrated and renewed quickly (e.g. salmon rivers, *Oncorhynchus spp.*), foraging efficiency is likely impaired by social behavior at high densities (McLellan 1994). However in systems where food is more evenly distributed (e.g. berries), food depletion at high population densities may be more significant (Welch et al. 1997). 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).

Population density also affected male reproductive success, because the number of offspring produced per male increased with increasing population density (paper III). This pattern may be related to the expansion of the Scandinavian bear population (Swenson et al. 1995). Swenson et al. (1998a,b) showed that the relative density of females declined more rapidly than for males from the center of the reproductive area towards the edge and that males dominated low-density areas into which bears are expanding. The declining female density towards the population edge decreases the

chances for males to obtain mating opportunities and therefore also their reproductive success.

Multilocus heterozygosity and internal relatedness

Multilocus heterozygosity refers to the fraction of loci within an individual that are heterozygous, and correlations between individual fitness and heterozygosity have been reported, although the topic remains controversial (Brittain 1996). We did not find a relationship between multilocus heterozygosity and either yearling body size or adult female body size (paper I, II). In other mammals, studies of red deer (Slate and Pemberton 2002), harbor seals (Coltman et al. 1998), and black-tailed prairie dogs (*Cynomys ludovicianus*) (Foltz et al. 1988) have shown a positive relationship between multilocus heterozygosity and juvenile mass. But Curik et al. (2003) found no large overall effects of microsatellite heterozygosity on morphological traits in adult horses (*Equus caballus*).

We found a negative relationship between internal relatedness (IR), which is an index of multilocus heterozygosity, and male reproductive success and female mate selection in brown bears (paper III, IV). Negative values of IR are suggestive of relatively outbred individuals, whereas high positive values suggest inbreeding. Individual heterozygosity at key or many loci may be reflected in male physical qualities and condition-sensitive traits (Brown 1997). Some of these traits may directly benefit males in competition. However, heterozygosity may also be selected via female choice; a female might choose the most heterozygous male through physical cues because it may favor the production of diverse and superior offspring. Less inbred, and thus more heterozygous males may also have an advantage in sperm competition (Andersson 1994). In red deer lifetime breeding success for both males and females was positively correlated with heterozygosity (Slate et al. 2000).

Cohort effects and environmental conditions

Available nutrition is probably the most important factor affecting growth (Laws 1956). In paper I we found a cohort effect on yearling body size, and in paper II we found that the environmental conditions experienced as a subadult (1-3 years of age) affect adult female body size.

Both the cohort effect and the environmental conditions experienced were probably related to different food availability among years (Nilsen 2002). Brown bears, which are typical capital breeders, rely largely 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 muscle to meet their own metabolic needs, as well as the energetic costs associated with gestation and lactation during hibernation. Food availability during the year the cubs-of-the-year are born, influences lactation during summer and fall as well as the offspring's 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.

Effects of cohort variations and environmental condition on body mass or size are often related to population density (e.g. Pettorelli et al. 2002, Solberg et al. 2004), and the effects of population density experienced as young can be transferred into adult age (Pettorelli et al. 2002, Solberg et al. 2004). Our results suggest these effects do not persist throughout life for female brown bears, because yearling body size was not important in explaining adult size (paper II). Atkinson et al. (1996) found a positive relationship between growth early in life and adult body size in polar bears. These differences in two closely related Ursid species may be related to environmental and food conditions. Polar bears live in a highly variable arctic environment and feed primarily on different seal species, which are unevenly distributed both temporally and spatially (Atkinson et al. 1996). However Scandinavian brown bears feed mainly on moose (*Alces alces*) and ants (*Formica spp.*, *Camponotus spp.*) in spring and on berries (*Vaccinium spp.* and *Empetrum hermaphroditum*) during summer and autumn (Dahle et al. 1998). Also the distribution of these food sources can vary in both time and space (Kardell and Eriksson 1990), however most likely not to the extent as for seals. In addition, Nilsen (2002) has shown that Scandinavian bears can compensate for crop failure of one berry species by eating more of other berry species. This may enable subadult female brown bears to show compensatory growth, whereas subadult female polar bears are less able to compensate for initially small body size.

Sexually selected infanticide and female reproductive strategies

Darwin (1871) pointed out that killing unrelated juveniles is advantageous for males if females then come into estrous earlier, offering the infanticidal male an immediate chance for reproduction. Hrdy (1974) observed in langurs (*Semnopithecus entellus*) that when a dominant male in the group was replaced by an immigrant male, many of the offspring sired by the former male soon disappeared and their mothers came in estrous and mated with the new dominant male. Based on these observations, Hrdy (1979) formulated a theory of sexually selected infanticide, where males kill dependent offspring, but not their own progeny, to gain access to breeding opportunities with the mother. Commonly stated requirements of SSI are that: 1) infanticidal males should not kill their own offspring; 2) death of the offspring should shorten the interbirth interval of the mother, and 3) infanticidal males should mate with the mother of the dead offspring and sire her next offspring (Hrdy 1979, Swenson 2003). Swenson et al. (1997, 2001) have observed that the killing of an adult male bear results in an increased cub loss 1.5 years later in Scandinavia, and attributed this to SSI. In addition, Bellemain et al. (2005a) found that all the theoretical requirements of SSI were fulfilled in Scandinavian brown bears. However, the occurrence of SSI, its operating mechanisms, and its potential effects on populations have become a controversial topic among bear researchers and managers (Swenson et al. 1997, 2001, Swenson 2003, Miller et al. 2003, McLellan 2005, paper IV, V, VI)

Sexually selected infanticide can influence mating systems (Wolff and Macdonald 2004). Based on the assumption that female bears may be choosy in selecting a male as the father of their offspring, they may be faced with a “dilemma” in areas where SSI is prevalent: on the one hand a female should try to select the “best” male, however on the other hand she should try to avoid having her young killed. It has been proposed that female brown bears use promiscuity as a counterstrategy to SSI (Swenson 2003, Bellemain et al. 2005a). In paper IV we found that females seemed to select males as father of their offspring according to their body size, age and genetic criteria. However we found indications that female mating behavior may also be influenced by the occurrence of SSI, as the geographically closest males, i.e. potentially infanticidal males, were significantly more often fathers. We suggest that females may choose to mate with as many close males as possible, but that they may be able to exercise a post-copulatory cryptic choice of the father of her offspring, which

could be viewed as making “the best of a bad job” (Wolff and McDonald 2004). In brown bears, both sexes roam to mate over large distances (Dahle and Swenson 2003), thus individuals whose home ranges centers are separated by 40 km can easily meet. Therefore we are confident that our results concerning the selection of geographically closest males is not due to bias, i.e. if females would come into contact with the closest males more frequently than with more distant males. However, we cannot exclude the possibility that choosing the closest males also reduces the cost of searching for potential mates, and this may partly explain the effect of distance on female choice.

The large size dimorphism in brown bears reveals the importance of intra-sexual selection, through male-male competition, for gaining access to females (Anderson 1994, paper III). In paper IV we focused on female mate selection in brown bears, based on the background that, in mammals, females are the more selective sex, and, in species with induced ovulation, females might be able to control paternity. Our results are consistent with the female choice hypothesis; however they do not exclude a role of males in determining paternity, because male-male competition can also occur during the post-copulatory phase via sperm competition (Ginsberg and Huck 1989). It is extremely difficult to distinguish between those two aspects of sexual selection and to evaluate their relative importance. Sperm selection by females (oocytes selecting sperm bearing compatible genes; e.g. Ehlers et al. 2000) can only be differentiated from sperm competition (the fittest sperm outcompete the other sperms; Gomendio and Roldan 1993) under controlled conditions (e.g. Hugues et al. 1999).

Female aggressiveness during lactation is aimed at protecting offspring (Maestriperi 1992), and female brown bears fight to protect their cubs against infanticidal conspecifics (McLellan 1994, Swenson 2003). Offspring defense, especially against infanticidal males, is potentially very dangerous for females, as has been shown in lions (*Panthera leo*). Also in bears, mothers are severely injured or killed by conspecifics while defending their offspring (Rogers 1987; Garshelis 1994; McLellan 1994, 2005). We found a decreasing probability of cub loss with increasing litter size, which in the presence of SSI is best explained by litter-size dependent variation in maternal offspring defense (paper V). This is consistent with the predictions of the parental investment theory and suggests that females adjusted their defense intensity according to the reproductive value of their litter. This agrees with findings in other mammals, especially rodents (e.g. Maestriperi and Alleva 1991;

Koskela et al. 2000; Jonsson et al. 2002). Anecdotal field observations support the hypothesis of reduced maternal defense activity for singleton litters in brown bears (Troyer and Hensel 1962). Our results strongly suggest that female brown bears defending large litters have a greater risk of being killed by conspecifics than mothers with a singleton litter, as only females with 2- or 3-cub litters were killed by conspecifics.

We found that singleton brown bear cubs had a higher mortality than cubs from larger litters. An explanation in contrast to the parental investment theory for this finding may be, that a mother abandons single offspring if she has the possibility to produce a second, larger litter within a short time (Tait 1980). The results of our model calculations showed that if abandonment of singletons would be used as a reproductive strategy, the advantage would be negligible (0.04%) for females with a 2-year reproductive cycle and small (0.97%) for females with a 3-year reproductive cycle. In comparison, Tait's (1980) original result was a 2.1% improvement in the expected number of offspring. Generally, opportunistic abandonment should only be used by young and never by old mothers, because only young mothers could increase their lifetime fitness by opportunistic abandonment. Therefore a female close to senescence should not abandon even a singleton. In addition, an old female could not be sure about her future reproductive possibilities or even her own survival. Due to the very low and age-dependent gain in fitness it seems unlikely that opportunistic abandonment as a reproductive strategy is selected for. Therefore, we rule out opportunistic abandonment, as suggested by Tait (1980), as a major cause of cub loss.

Primiparous females often have fewer and smaller offspring than multiparous females (Clutton-Brock 1991, Festa-Bianchet et al. 1995). They may also lack refined behavioral skills associated with foraging (Becker et al. 1998) and parental care (Wang and Novak 1994), which may be of special importance for defending offspring against SSI. In paper VI we found that a mother loses more offspring when primiparous than when multiparous. The probability of cub loss of primiparous females was positively correlated to male turnover (a variable predicting SSI). We found no relationship with environmental conditions (Swenson et al. 2001), as has been suggested for brown bear cub survivorship in Alaska (Miller 2003). SSI seems to be the major factor causing cub loss of primiparous females, which is also supported by the timing of cub loss, because most cubs were lost during the mating season. That primiparous mothers lose more cubs than multiparous females suggests that

primiparous mothers are less experienced or efficient in defending their cubs against infanticidal males.

The probability of cub loss in primiparous females was suggestively and negatively correlated to female age at primiparity. Females in the south reached primiparity earlier (4 years) than females in the north (5 years), however the age of first successful litter in both study areas were very similar (5 years; Swenson et al. 2001). The differences in age of primiparity between the study areas may be related to the more favorable environmental conditions in the south, which may enable females to reach primiparity earlier, however it remained unclear why females primiparous at age 4 have a higher probability of cub loss. This result was not related to a larger body size of females that were primiparous at later ages, because body size at primiparity did not influence the probability of cub loss. It may be that in a population where SSI is a major source of cub mortality, an additional year of experience with other bears may provide a better knowledge of local dominance hierarchies or more experience in avoiding potentially infanticidal individuals, which increases a young females' chance of successfully raising a litter. From the point of view of lifetime reproductive success, it may be an advantage for young female brown bears to reproduce as early as possible, because male turnover is unpredictable in space and time.

In our southern study area, females that remained philopatric were primiparous at an older age than dispersing females, which indicates a social suppression of reproduction of philopatric daughters residing within their mother's home range. Related female brown bears often live in matrilinear assemblages (Støen et al. 2005). Due to the extensive overlap of home ranges within matrilinear assemblages, dominance hierarchies can develop among related females and reproductive suppression can be seen as a means to reduce resource competition, as found in badgers (*Meles meles*) (Woodroffe and MacDonald 1995). Also in bears dominance hierarchies have been observed (Pulliainen et al. 1983), especially when they aggregate at concentrated food sources (Craighead et al. 1995a, Gende and Quinn 2004). Female brown bears have been observed killing the offspring of other females (Hessing and Aumiller 1994, McLellan 1994), thus the threat of infanticide for subordinate females could result in delayed reproduction until such time that the female could successfully rear offspring, as proposed for other species (Wasser and Barash 1983, Wolff 1997). Because the home ranges of unrelated females overlap less than those of related females (Støen et al. 2005), natal-dispersing females surrounded

by unrelated females probably have less contact with other females. With less contact between the females, a hierarchy may not develop and these females may thus be relieved from reproductive suppression.

Inbreeding avoidance (Wolff 1992) was most likely not a mechanism for reproductive suppression, because we found no significant difference in the age of primiparity between females that dispersed outside their father's home range and those that overlapped with their fathers until primiparity. Due to the low sample size in this study we cannot entirely rule out the importance of the father's influence. However, empirical data show only 2% incestuous matings (reproduction between daughter and father) (paper IV).

The question arises about why females should remain philopatric, when dispersal is positively related to a lower age of primiparity. In paper VI we found suggestive evidence that females primiparous at an older age lost fewer cubs. There also may be other a fitness advantages of philopatry, such as improved survival of the female, familiarity with the local area and neighbors, proven resource base, and benefits of kin selection (see Wiggett and Boag 1990), that exceed the disadvantage of delayed primiparity. It remains unknown, however, whether or not fitness is increased by philopatric behavior in brown bears.

Human induced life-history patterns

Selective harvesting causes phenotypic evolution in exploited populations (Laws 2001 etc). Although the heritability of life-history traits is much lower than that of morphological traits (Mousseau and Roff 1987), it is large enough to bring about genetic change under selective exploitation (Law 2001). Experimental size-selective harvesting of fish populations has shown evolutionary effects on somatic growth and population productivity (Conover and Munch 2002), and life-history traits of fish can change rapidly when under strong selection (Reznick et al 1990).

Persecution by humans is the major reason for the decline and the extinction of the brown bear in many parts of the world (Servheen et al. 1999, Swenson et al. 2000). However, the duration of persecution of brown bears by humans differed between Europe and North America. To reduce depredation, early policy in historic Europe was to exterminate bears (Zimen 1990, Swenson et al. 1995) and extermination efforts were carried out with primitive weapons and traps until effective firearms became

available in the 19th century. Extermination was therefore a slow process until their extinction or near extinction in most European countries (Swenson et al. 2001). In North America persecution by settlers with modern weapons caused the distribution of brown bears south of Canada to collapse rapidly from 1850-1920 and most of the remnant populations disappeared during 1920-70 (Mattson and Merrill 2002). Although many remnant populations in Europe have increased greatly in size and distribution in the past 50-100 years, the range of brown bears has increased in only a few places in North America (Servheen et al. 1999).

High levels of human persecution for more than 50 generations apparently have contributed to an evolutionary life-history change in brown bears, with females investing relatively more in reproduction in relation to body size and mass, apparently affecting litter size, litter interval and age of primiparity. As a result, brown bears in Europe have the highest documented reproductive rates (Sæther et al. 1998). Although human-induced evolution is probably often negative for the affected population over the long term (Coltman et al. 2003, Harris et al. 2002), the life-history changes resulting from human-induced selection have probably allowed brown bears to survive in many human-dominated landscapes of Europe and even flourish with modern wildlife management in a number of European countries (Linnell et al. 2001, Zedrosser et al. 2001). The lower reproductive rates of North American brown/grizzly bears make them less able to survive in human-dominated landscapes. Behavioral traits may also have been subject to human selection, because European brown bears are less aggressive to humans (Herrero 1985, Swenson et al. 1999) and less diurnal (Huber and Roth 1993) than North American bears, which also make them easier for humans to tolerate.

It seems to be a fact that in our modern world the vast majority of brown bears dies because humans kill them (Sandegren and Swenson 1997, McLellan et al. 1999, Schwartz et al. 2005). Above we have presented evidence that humans may have changed brown bear life-history due to their long-term persecution. But we have also found evidence that humans can have short-term impacts on the mating system and patterns of reproductive success of brown bears as well. Illegal killing has changed the male age structure in our northern study area (Swenson et al. 2001, Swenson 2003). Our analysis of male annual reproductive success (paper III) indicated that age was more important for male annual reproductive success in the north and body size was more important in the south. Body size and age of male brown bears are highly

correlated in our study areas (paper IV). The study area differences in the importance of body size and age were likely related to the aforementioned differences in male age structure due to human influence in the study areas. A single old male dominated the reproduction in the north during the study period, which probably resulted in the relatively higher importance of age in the north. In the south, the area with the more even male age structure, no single male was able to dominate reproduction in this way, probably due to more intense competition among males, with body size as the deciding factor.

Perspectives

A PhD thesis may answer some questions regarding a certain topic. However, a maybe even more important contribution is the multitude of new questions that may arise from it. This has been the case with this thesis. The life-history of brown bears and large carnivores in general has barely been investigated and a whole new world of interesting questions stretches ahead of us (isn't that wonderful!). Below I would like to present some ideas arising from this research.

Life history patterns are one of the underlying principles that drive reproductive success, sexual selection and evolution itself. Today's life history theory has been developed in fish, birds and small mammals. In large mammals, life-history research has been carried out primarily in ungulates, and very little is known about the life history of large carnivores. However ungulates and large carnivores, although closely connected in their roles as predator and prey, show some fundamental differences in their ecology, behavior, and functions in the ecosystem. These differences may be reflected in their life history patterns. Understanding these differences, if there are any, would break new scientific ground, improve our evolutionary and biological knowledge, as well as result directly in better management of species and biological diversity.

Research results from the Scandinavian Brown Bear Research Project have suggested for the first time, that SSI operates in a non-social species. This has been further confirmed in this thesis. Hypotheses have been proposed about how SSI operates in brown bears (McLellan 2005). Currently we are not able to test these hypotheses, but maybe in the future, with increased data and the help of GPS radio-

collars and improved genetic methods, some of these hypotheses may be tested, or maybe new mechanisms discovered. Considerable controversy exists among managers and bear biologists about the effect that SSI might have on populations, population growth, bear hunting, and ultimately management of a species with large conservation interest. For example, does the killing of adult males have an effect on population growth, or how does SSI influence the lifetime reproductive success of females? The concept of SSI is also starting to gain increased interest in other solitary large carnivore species (e.g.: wolverines (*Gulo gulo*), cougars (*Felis concolor*), leopards (*Panthera pardus*)), all of them charismatic species with large management and conservation interests. Increased knowledge about SSI may be especially important for the conservation and management of small bear and other large carnivore populations.

Reproduction is a major event in the life history of any individual, and consists of several different components, such as age and size at maturity, and age- and size-specific reproductive investment. Understanding the mechanisms that influence the reproductive success of individuals is essential to understanding the mechanisms for natural selection. Consequently, analyzing the factors related to individual variation in reproductive success, and identifying the characteristics of successful individuals, gives insight into the selective pressures affecting evolutionary processes, especially if studied over an individual's lifetime. Evaluating these factors in a lifetime perspective would contribute to better knowledge, not just about bears, but sexual selection theory generally. Longevity is also a major factor influencing lifetime reproduction, and 95% of all brown bear mortalities are human-caused in Scandinavia. However little is known about whether human-caused mortality is associated with life-history patterns.

Human activities have affected the abundance and distribution of many species and drastically altered ecosystems, sometimes in radical ways through habitat destruction, other times in more subtle ways by altering species compositions or changing the sex/age structure of populations (Festa-Bianchet 2003). The conservation and management of large carnivores is often highly controversial. Large carnivores compete with man for livestock and game animals, thus causing economic damages, and even occasionally wound or kill people. On the other hand, large carnivores are often used as "umbrella species" for conservation purposes and raise high emotional responses (positive and negative) in the media and the public. We need to better understand if and how humans are shaping animal species by studying

to what degree human harvesting is selective in brown bears, to what degree life-history parameters are heritable, and to what extent human harvesting may be an evolutionary factor for brown bears.

A common tendency in the management and conservation of species and populations has been to overlook individual differences by treating populations as homogeneous units. However the overall dynamic behavior of populations must ultimately be understood in terms of the behavior of individuals. Preliminary results of our research suggest that the loss of certain individuals has little demographic impact, whereas the presence or absence of certain other individuals can have cascading effects that impact behavioral patterns, spatial distribution, dominance hierarchies and survival of offspring. The future survival of many carnivore species in human-dominated landscapes will only be able under strict control by humans. In the future it will become more important to include behavioral ecology, behavioral and life history concepts into wildlife management, which has so far mostly been ignored by managers.

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Those who do not stop asking silly questions become scientists. –
Leon Lederman

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Paper I

“You have to do your own growing now matter how tall your grandfather was.”–
A. Lincoln

Correlates with body size and mass in yearling brown bears

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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 3 offspring, where the heaviest yearling was on average 29.5 ± 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 age 1 to 3 increased with increasing yearling body size.

Key words: body mass, maternal investment, population density, litter size, *Ursus arctos*

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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 prior to the separation from their mothers varies considerably in many species, e.g. alpine marmots (*Marmota marmota*) (Allaine, Graziani & Coulon, 1998) and polar bears (*Ursus maritimus*) (Derocher & Stirling, 1998a). 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 size and mass of yearling brown bears (*U. 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, 2003a). In brown bears reproductive longevity was thought to approximate physical longevity (Pasitschniak-Arts 1993), but new data presented by Schwartz *et al.* (2003b) 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 only have focused on body mass. We measured the brown bears at the 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. Based on the available literature we considered 7 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, Bijmens & 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, 1998a; 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). Due to ethical reasons (to avoid drowning and overheating) and for practical reason (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 (Table1).

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; Sydean *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 and Stirling (1998a) reported that offspring size increased from the onset of reproduction before subsequently decreasing from the age of 15 years. Based on 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 (see Lloyd, 1987 and Roff, 1992 for reviews). 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 (1998a) found that the difference in body mass between siblings in triplet litters was approximately 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. Based on the findings of Derocher & Stirling (1998a) 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, 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

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 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), and we also expect maternal expenditure to decrease at high population densities as food resources should be limited when the population approaches the 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 midsummer (Farley & Robbins, 1995). Preliminary analyses suggest that yearling body mass differs among cohorts (Swenson, Dahle & Sandegren, 2001a). 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) is generally positively associated with offspring size and mass. Therefore we predicted (9) that subadult survival (one to three 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 (approximately 61° N, 14° E, southern study area), and in Norbotten County, northern Sweden (approximately 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 approximately 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 (*B. pendula*), aspen (*Populus tremula*) and grey alder (*Alnus incana*) are common. The elevations range from about 200 m a.s.l. in the southeastern part to about 1.000 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° C 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 ~ 600-1.000 mm annually (Lundqvist, 2002). Bears are intensively hunted in the entire area.

The northern study area (north) encompasses 8,000 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 2.000m. The valleys are dominated by mountain birch, Scots pine and Norway spruce. Mountain birch forms the tree line and occurs at a maximum elevation of 600 m a.s.l (Grundsten, 1997). The mean temperatures in January and July are -13° C and 13° C, respectively. Snow cover lasts from beginning of October until late May, and the vegetation period is about 110-130 days (Moen 1998). Average precipitation is ~ 500-1.000 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). Due to the differences between the study areas we controlled for study area in the analysis.

Capture and handling

Yearling brown bears and their mothers were immobilised 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 radiomarked 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). Body mass of immobilised 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 radiotransmitters attached to neck collars (Telonics model 400). 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 due to 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 km²) was estimated in both the north and 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 based on 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 scats 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 due to the less harsh environment, the population densities could be regarded 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 controlling 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](http://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 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; 2001b), before the lactation peak during summer (Farley & Robbins, 1995). For this reason statistical analyses were carried out twice, using both litter size in spring (yearlings counted after the family group leaves the den) and in fall (cubs-of-the-year counted before the family group entered 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 (Swenson *et al.*, unpublished 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 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 ± 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 ($F = 0.341$, $df = 1$, $P = 0.564$).

Yearling body size and mass were positively related to maternal size (Tables 1, 3 and 4). Maternal age did apparently 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: $\beta = 1.988 \pm 1.025$, $df = 145$, $t = 1.940$, $P = 0.054$; mass: $\beta = 4.882 \pm 2.096$, $df = 143$, $t = 2.329$, $P = 0.021$), which decreased in strength with increasing maternal size (size: $\beta = -0.033 \pm 0.017$, $df = 145$, $t = -1.970$, $P = 0.051$; mass: $\beta = -0.083 \pm 0.034$, $df = 143$, $t = -2.417$, $P = 0.017$), however these models had AIC_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 AIC_c 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 models 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 $t = 6.612$, $df = 39$, $P < 0.001$). 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, $n = 10$, or mixed sex, $\bar{X} = 3.0 \pm 0.5$ kg, $n = 18$, $F_{2,37} = 0.692$, $P = 0.514$). In triplet litters there was also variation in body mass within a litter (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 ± 2.8 % and 2.8 ± 0.4 kg or 12.2 ± 2.2 %, respectively, $t = 4.483$, $df = 75$, $P < 0.001$, Table 1). Body mass of all littermates in quadruplets was only obtained in 2 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 $t = 3.422$, $df = 17$, $P = 0.003$). 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 ($F = 1.834$, $df = 1$, $P = 0.179$ and $F = 0.394$, $df = 1$, $P = 0.534$, 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 AIC_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 ($t = 2.021$, $df = 144$, $p = 0.045$, $AIC_c = 0.424$).

Body size and mass of yearlings varied among cohorts, and did not co-vary in the 2 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 $SD = 3.263$ for yearling size and mass, respectively) was almost as great as between-mother variation ($SD = 1.801$ and $SD = 4.670$, respectively).

One hundred twenty yearlings were tracked by radio telemetry until the age of three years. Fourteen individuals died during this time period due to 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 was 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 *Mirounga leonina*, Arnborn *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 AIC_c values of models including this term). The most likely explanation is that our sample included only 5 females older than 14

years, the age at which offspring size started to decrease in polar bears (Derocher & Stirling, 1994; Derocher & Stirling, 1998a). 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) which has been reported in several species (e.g. Foltz, Hoogland & Koscielny, 1988; Allaine *et al.*, 1998; Derocher & Stirling, 1998a). Also as predicted (4), within-litter variance in offspring body mass increased with litter size. Derocher & Stirling (1998a) 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 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 fed 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 (1998a) 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 disproportionately in males could increase mortality of female cubs. Survival of

subadults (one-three 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; 2001b; Zedrosser *et al.*, unpublished data). Thus, to the extent maternal investment in different sexes are 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 to 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, so 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 four-fold 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 pre-denning 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 for meeting 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 they 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*, *V. 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 are 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 are 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 (A. Zedrosser *et al.* in press).

Dahle & Swenson (2003a) analyzed 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), 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.*, unpublished 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 to 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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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 (one to three years old) is positively related to yearling size and mass.	yes

* limited support

Table 2. Mean head circumference (cm) and body mass (kg) of brown bear yearlings in Sweden. Litter size is the number of cubs-of-the-year the previous fall. Means are presented with \pm one standard error.

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

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

Explanatory variables	<i>P. estimate</i>	<i>SE</i>	<i>t</i>	<i>P</i>
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

^a parameter estimates are not given due to the large number of estimates (see text).

^b F statistics (type III).

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

Explanatory variables	<i>P. estimate</i>	<i>SE</i>	<i>t</i>	<i>P</i>
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

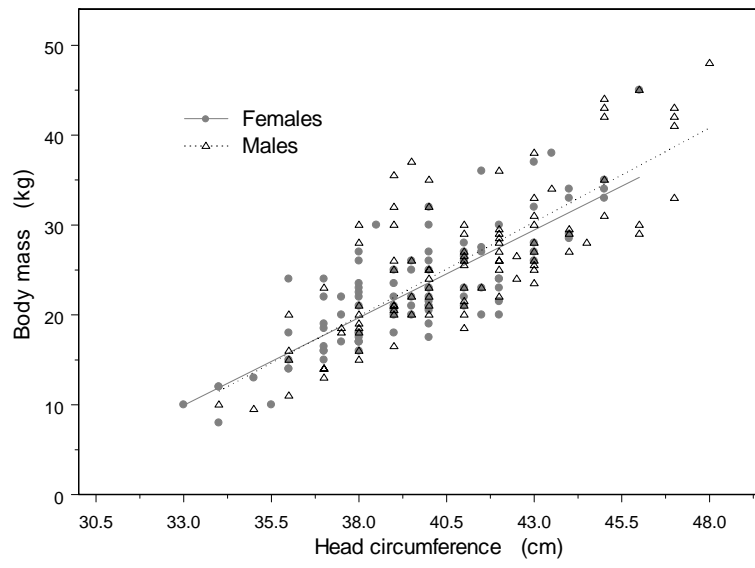
^a parameter estimates are not given due to the large number of estimates (see text).

^b F statistics (type III).

Figure legend

Figure 1. The relationship between head circumference and body mass of male and female yearling brown bears with the least squares regression lines.

[Fig. 1. Dahle *et al.*]



Paper II

”Size does matter!” –
Pamela Anderson

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

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

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

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

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

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

Surrogates for individual fitness have been reported to correlate with multilocus heterozygosity, however the topic remains controversial (Britten 1996). Significant multilocus heterozygosity-fitness correlations have been found in birds (e.g. Hansson et al. 2001) and mammals (e.g. Coltman et al. 1998, Slate et al. 2000). Coltman et al. (1998) examined the relationship between fitness-related traits and microsatellite heterozygosity in wild harbor seal pups (*Phoca vitula*) and found that birth mass was positively influenced by individual heterozygosity.

In large mammals, research on growth and its determinants has almost exclusively been carried out in ungulates (e.g.: Solberg et al. 2004, LeBlanc et al. 2001, Toïgo et al. 1999), and little is known about this subject in large, terrestrial carnivores, except for some research in polar bears. The understanding of population dynamics of large ungulates is limited not by the lack of models and theories, but by the availability of data on natural populations (Eberhardt 1985, Gaillard et al. 2000). This is even more relevant for large carnivores, a group of animals

that is excessively difficult to study. They are often secretive, difficult to capture, and have a long life span and long intervals between reproductive events. Our 20-year study of brown bears (*Ursus arctos*) in two study areas in Scandinavia allows us to investigate these questions, because we have followed individuals from birth until death and taken repeated measurements of body size of marked animals as juveniles and adults.

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

Male reproductive success in polygynous, size-dimorphic species is dependent on body size (Andersson 1994), and males probably have been selected to maximize growth rate (Clutton-Brock et al. 1988). In contrast, females in size-dimorphic species have to trade growth for reproduction and cannot grow as fast; several studies have suggested different growth patterns between males and females in ungulates (e.g.: Festa-Bianchet et al. 1994, LeBlanc et al. 2001, Toïgo et al. 1999). Brown bears exhibit a polygynous mating system and strong sexual size dimorphism (Schwartz et al. 2003). We therefore restrict our analysis to female brown bears only. We investigated the growth patterns of female brown bears with the von Bertalanffy growth curve (von Bertalanffy 1938), and investigated four factors that are likely to determine female adult body size: population density, food conditions, size at weaning, and multilocus heterozygosity. Specifically, we predicted that adult body size of female brown bears is 1) negatively related to population density; 2) positively correlated to the food conditions experienced as a subadult; 3) positively correlated with yearling body size, 4) and positively correlated with multilocus heterozygosity.

MATERIAL AND METHODS

Study area and study populations. The study areas were in Dalarna and Gävleborg counties in south-central Sweden (approximately 61° N, 14° E, southern study area), and in Norbotten County, northern Sweden (approximately 67° N, 18° E, northern study area). Both areas are close to the northern and southern edges of the range of the Scandinavian brown bear population and are approximately 600 km apart. The southern study area (south) consists of 13,000 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*), European aspen (*Populus tremula*) and gray alder (*Alnus incana*) are common. The elevations range from about 200 m in the southeastern part to about 1,000 m in the western part, but only a minority of the area is above timberline, which is about 750 m elev. The mean temperatures in January and July are -7° C and 15° C, respectively. Snow cover lasts from late October until early May and the vegetation period is about 150-180 days (Moen 1998). Average precipitation is ~ 600-1.000 mm annually (Lundqvist 2002). Bears are intensively hunted in the entire area.

The northern study area (north) encompasses 8,000 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 2,000m. The valleys are dominated by mountain birch, Scots pine and Norway spruce. Mountain birch forms the tree line and occurs at a maximum elevation of 600 m (Grundsten 1997). The mean temperatures in January and July are -13° C and 13° C, respectively. Snow cover lasts from beginning of October until late May, and the vegetation period is about 110-130 days (Moen 1998). Average precipitation is ~ 500-1,000 mm annually (Påhlson 1984). Bears are protected in the national parks, but hunted in the surrounding areas.

Capture, handling and body size measurements. Lone female brown bears and females with yearling cubs were immobilized with a dart gun from a helicopter in mid-April in the southern study area and early May in the northern study area, shortly after den emergence. We used 2.5 mg tiletamine, 2.5 mg zolazepam (Zoletil®, Virbac, Carros, France) and 0.02 mg medetomidine (Domitor®, Orion Pharma Animal Health, Turku, Finland) per kg to immobilize the bears. Atipamezol (Antisedan®, Orion Pharma Animal Health, Turku, Finland) was used as an antidote for medetomidine (5 mg per 1 mg medetomidine) (Kreeger et al. 2002). A tissue sample was taken for genetic analysis. Body length in cm was measured from the tip of the nose to the caudal end of the last vertebrae in the tail. The head

circumference in cm (at the widest part of the zygomatic arch between eyes and ears) was measured with a tape measure and used as a surrogate measure of overall size of a female. In our study we used only females of known age, which we had followed from yearling to adult age. Female brown bears can start producing litters at the age of four years (Schwartz et al. 2003); we therefore defined a female as an adult if it had reached at least this age. For ethical reasons we did not capture females with cubs of the year, and thus not all females were measured at the same adult age. We therefore corrected for age in our statistical analysis. Because all bears were captured within a 2-week period in each study area, we did not adjust body size for capture date. All capture and handling conformed to the guidelines established by the American Society of Mammalogists (Animal Care and Use Committee 1998) and the current laws regulating the treatment of animals in Sweden and were approved by the appropriate Swedish ethical committee (Djuretiska nämnden i Uppsala).

Individual population density index, northern study area.—From 1995 to 2002 virtually every adult male and female and all subadult female bears were radio-marked in the north (Swenson et al. 2001). We calculated the arithmetic mean of the radio-locations of every radio-collared adult and subadult bear in the year 2002 (the year with most radio-marked individuals). From this mean center we calculated the distance to the arithmetic mean centers of all other radio-marked bears throughout the entire study period. We then counted the number of bears (adult males and females and subadult females) surrounding a given individual within a certain radius. We chose a radius of 17.84 km because it approximates an area of 1000 km² commonly used as the basis of density measure for bears (McLellan 1994); the median adult male home range was 833 km² in this area (Dahle and Swenson 2003). The number of cubs present per adult female was estimated by dividing the mean litter size in our northern study area (2.4; Swenson et al. 2001) by the mean litter interval (2.6 years; Swenson et al. 2001), which resulted in an estimated 0.92 cubs present per adult female per year. Because no radiomarked subadult males were represented in the initial count of bears surrounding a given individual, we multiplied the number of subadult females by 2, assuming an even sex-ratio (Bellemain et al. 2005). The individual density index I_d in a radius of 17.84 km was calculated as $I_d = N_{ad.m} + 1.92N_{ad.f} + 2N_{subad.f}$, where $N_{ad.m}$ is the number of radio-marked adult males, $N_{ad.f}$ is the number of radio-marked adult females and $N_{subad.f}$ is the number of radio-marked subadult females. Using the software ArcView GIS 3.2a (Environmental Systems Research Institute, Inc., 1992-2000, Redlands, California, USA) we

subtracted the area within the 17.84 km radius around a bear that extended beyond the borders of our study area, and extrapolated the number of bears to an area of 1000 km².

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

Individual population density index, southern study area.—A population size estimate, based on a DNA analysis of non-invasive sampling of scats, was carried out in the south in 2001 and 2002 (Bellemain et al. 2005). We have used these results as a basis to calculate an individual density index around each individual in our analysis. For each radio-collared bear, we counted the number of genetically identified individuals within a 17.84 km radius, based on the centres of the locations of all scat samples for each individual. Also here we chose a radius of 17.84 km; the median adult male home range was 1055 km² in this area (Dahle and Swenson 2003). Bellemain et al. (2005) found that 71% of all radio-collared bears in the southern study area were represented in the genetic sample. To account for the individuals not detected in the non-invasive population sampling, we divided the individual density index by 0.71. The resulting individual density index I_d thus can be expressed as $I_d = N_i / 0.71$, where N_i is the number of genetically identified individuals surrounding a radio-collared bear. We subtracted the area within the 17.84 km radius around a bear that extended beyond the borders of our study area using GIS maps, and extrapolated the number of bears to an area of 1000 km².

Sæther et al. (1998) estimated a population growth rate of about 16% annually in our southern study area for the period 1985-1995. Population size and density estimates based on aerial capture-mark-recapture techniques were carried out in the southern study area in 1993 (Swenson et al. 1995) and again in 2001 (Solberg and Drageset 2003). Both estimates yielded very similar results, suggesting that although the population in the general area had increased in size and range, densities in the intensive study area had stayed about the same in the period

1993-2001. To temporally correct the individual population density indices for this period, we assumed stable densities from 1993-2002. The temporally corrected individual population density index tI_d for an individual bear in year y (for $y < 1993$) was then $tI_d = I_d / 1.16^{(1993-y)}$, where I_d is the index for 2001-2002.

We are confident that these individual density indices are comparable between the northern and southern study area, because actual densities were estimated in both areas with high (~71%, south) to very high (~100%, north) proportions of marked animals in both cases.

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

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

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

$$s_a = S(1 - e^{-k(a-A)})^3$$

where s_a = head circumference (cm) at age a , S = asymptotic head circumference (cm), k = size growth rate constant (years^{-1}), A = fitting constant (extrapolated age at zero size)(years). Several individuals have been captured more than once during our study period; we used only the measurement taken at the highest age in our analysis.

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

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

RESULTS

Head circumference was used as a surrogate measure for overall size rather than body length, because head measurements may provide the most useful measures to compare populations in bears (Derocher and Stirling 1998) and it showed a lower coefficient of

variation ($CV = 0.174$) than body length ($CV = 0.185$) ($N = 525$, including recaptures). Both measures were highly correlated ($r = 0.944$, $P < 0.001$, $N = 525$), so a direct comparison with data published elsewhere is warranted.

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

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

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

DISCUSSION

Much (about 50%) of the individual variability in body size was explained by age, as expected because the species shows a multiyear growth pattern (Schwartz et al. 2003). However, once this effect was accounted for, we found significant positive effects of food conditions and negative effects of population density on adult size in female brown bears. We also found significant differences between the study areas. Females were larger and grew faster in the south. In addition we found significant interactions between study area and population density and study area and environmental conditions. In contrast to several studies of ungulates, we did not find a relationship between size as a young and as adult; i.e. females seemed to be able to compensate for size disadvantages at weaning. We also found no correlation between multilocus heterozygosity and adult size.

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

Overall population density appears to be related to food availability in bears (McLellan 1994), suggesting that food is the ultimate regulating factor. Density dependency may work by reducing the food base and/or increasing competition for food. In systems where food is highly concentrated and renewed quickly (e.g. salmon rivers, *Oncorhynchus*), foraging efficiency is likely impaired by social behavior at high densities (McLellan 1994). However in systems where food is more evenly distributed (e.g. berries), food depletion at high population densities may be more significant (Welch et al. 1997). 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 and Drageset 2003), suggesting

that the population was near or approaching carrying capacity or was held at that level by hunting. We found that the effect of density was stronger in the south than in the north, perhaps because the density was higher in the south (~30 bears/1000 km²) than in the north (~11 bears/1000 km²). Most likely due to the more severe environmental conditions, the carrying capacity may be lower in the north, which was also suggested by the interactions indicating that annual food abundance had a greater impact on adult size in the north. Our results support the physiological constraint hypothesis: adult female bears were smaller at high densities because their growth was limited by resource availability.

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

Dahle et al. (in press) have shown a significant cohort effect on yearling size in brown bears. Our results suggest these effects do not persist throughout life for female brown bears, because, contrary to our prediction, yearling body size was not important in explaining adult size. The relevant candidate model with the effect of yearling size on adult female size was neither significant nor did it show any trend (β of yearling size = 0.002, $P = 0.988$), when controlling for study area and age. Atkinson et al. (1996) examined the relationship between growth early in life and adult body size in polar bears. They found that adult body length was significantly correlated with length in two-year-old females (Atkinson et al. 1996). However we did not find a relationship between female yearling size and adult female size in brown bears. These differences in two closely related ursid-species may be related to environmental and food conditions. The polar bear lives in a highly variable arctic environment and feeds primarily on ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*), which are unevenly distributed both temporally and spatially (Atkinson et al. 1996). Hunting efficiency of subadult females may be less than for adults (Stirling and Latour 1978). Scandinavian brown bears feed mainly on moose (*Alces alces*) and ants (*Formica.*, *Camponotus*) in spring and berries (*Vaccinium* and *Empetrum hermaphroditum*) during summer and autumn (Dahle

et al. 1998). Especially the distribution and abundance of berries can vary in both time and space (Kardell and Eriksson 1990), however most likely not to the extent as for seals. In addition, Nilsen (2002) has shown that Scandinavian bears can compensate for crop failure of one berry species by eating more of other berry species and no specialized hunting skills are necessary. This may enable subadult female brown bears to show compensatory growth, whereas subadult female polar bears are not able to compensate for initially small body size.

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

We found that the effect of environmental conditions on growth and adult size in female brown bears was stronger in the north than in the south and that northern adults were smaller and grew more slowly. Kojola and Laitala (2001) investigated variations in body size of brown bears throughout Finland and found that male brown bears were larger in the south; however they were not able to document the same for females. McNab (1971) did not find statistically significant associations between latitude and skull measurements of brown bears in North America. Primary productivity and average temperatures that favor plant growth are higher in southern than in northern Scandinavia (Moen 1998), but forage quality may be better in climatically harsher environments (Albon and Langvatn 1992). In ungulates, nutritional quality can outweigh the effects of plant biomass on body mass (Langvatn and Albon 1986), but brown bears do not rely on browse like ungulates. In spring Scandinavian brown bears rely mostly on protein sources (moose, ants). Their capability to obtain enough nutrition for growth and store adipose fat tissue for hibernation relies to a large extent on the quality and abundance of berries during summer and autumn (Dahle et al. 1998), a food resource that varies in both time and space due to environmental conditions (Kardell and Eriksson 1990). Similarly, it has been suggested for polar bears that long-term climatic variation could affect growth patterns by altering availability or abundance of food (Derocher and Stirling 1998). The smaller body size of female brown bears in the north is most likely explained by the shorter growing season and the lower primary productivity there. In addition, northern females hibernate for 6.9-7.9 months, depending on their reproductive status, whereas in the south females hibernate 5.3-6.9 months (Manchi and Swenson 2005). Thus

southern females may be able to invest more energy into growth than in the fat accumulation necessary for hibernation.

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

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

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Figure legend

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

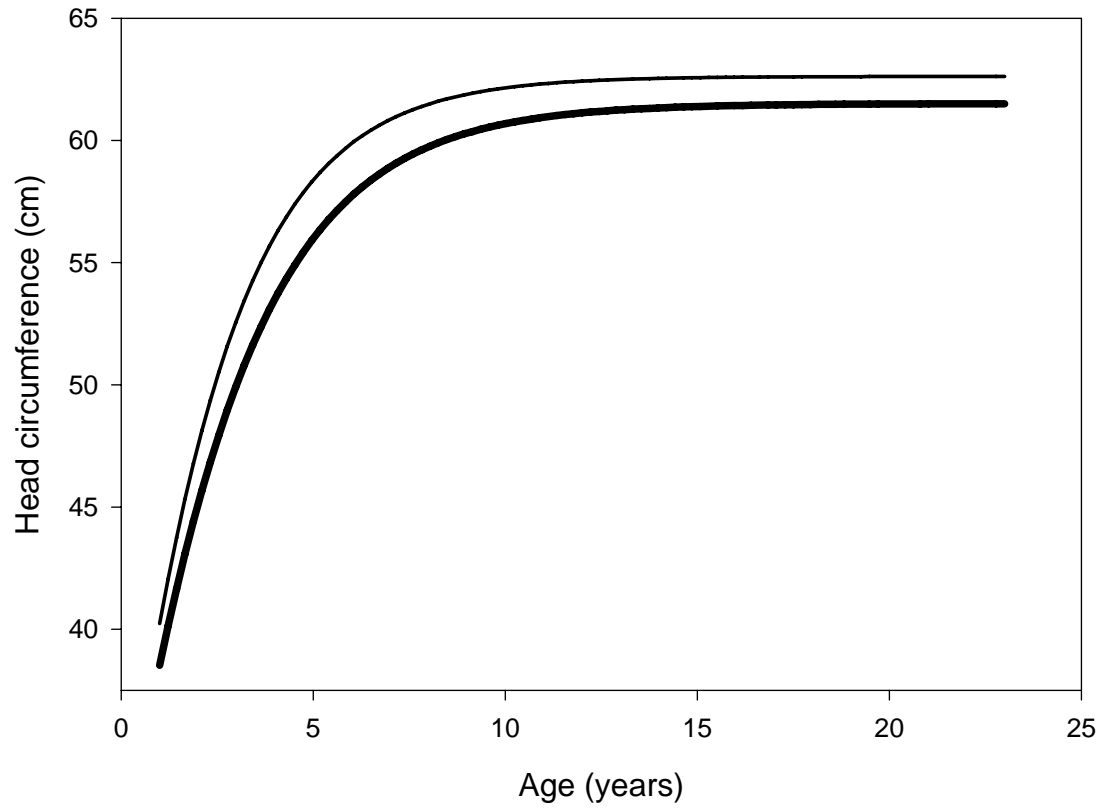
Table 1: Parameter estimates for the von Bertalanffy size-at-age curves for head circumference of female Scandinavian brown bears ($\pm SE$). S is the asymptotic head circumference, K is the size growth constant, and A is the theoretical age at which the animal would have size zero.

Study area	S (cm)	K (year ⁻¹)	A (years)	n
North	61.50 \pm 0.69	0.368 \pm 0.038	-4.01 \pm 0.49	68
South	62.62 \pm 0.49	0.445 \pm 0.034	-3.47 \pm 0.33	115

Table 2: Parameter estimates and test statistics for the general linear model explaining adult size in female Scandinavian brown bears. Df is degrees of freedom, β is the slope, SE is the standard error, t denotes the t-value, P denotes the significance level obtained by likelihood ratio tests (type III), R^2 is the percent variance explained by the model, $AICc$ shows the corresponding value of the entire model, and $\Delta AICc$ denotes the differences in AICc-values. Only models with AICc-values of ≤ 2 are shown. $N = 43$ (20 in the northern study area, 23 in the southern study area).

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

Fig. 1.



Paper III

“Be fruitful, and multiply.” –
Genesis 1, 22

Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density.

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Running headline: reproductive success in male brown bears

Summary

1. We studied male annual reproductive success (ARS) and its determinants (phenotypic characteristics, age, population density) in two Scandinavian brown bear populations, using molecular techniques to determine paternity.
2. We found a significant difference in male ARS between the study areas, with males producing fewer offspring annually in the south than in the north.
3. In general, older and larger males had higher ARS. Older males may be more experienced in competition for reproduction (male dominance). Large body size is of direct benefit in male-male competition and of advantage in endurance competition for the access to females.
4. Age was relatively more important for ARS in the north and body size was more important in the south, which may be related to differences in male age structure in the study areas due to illegal killing. A single old male dominated the reproduction in the north during the study period, and this most likely resulted in the relatively higher importance of age in the north. In the south, the area with the more even male age structure, no single male was able to dominate. This most likely resulted in a more intense competition among males, with body size as the deciding factor.
5. Male ARS was positively correlated with population density. This may be related to the structure of an expanding bear population, with female densities more than male density declining towards the population edge.
6. Internal relatedness, which is a measure of genetic heterozygosity, was negatively correlated with ARS, suggesting that outbred individuals have a higher ARS. Individual heterozygosity at key or many loci may be reflected in male physical qualities and condition-sensitive traits, and some of these traits may directly benefit males in contest or in sperm competition.

Keywords

Age, body size, brown bear, density, heterozygosity, annual reproductive success, *Ursus arctos*

Introduction

Understanding the mechanisms that influence the reproductive success of individuals is essential to understand the mechanisms under natural selection. Annual reproductive success (ARS) is a measure of fitness and can be defined as the total number of offspring produced in a year by each member of a set of known individuals (Grafen 1988). Consequently, analyzing the factors related to individual variation in ARS, and identifying the characteristics of successful individuals, gives insight into the selective pressures affecting evolutionary processes, especially if summed over a lifetime. ARS is usually not easy to study in natural populations of large mammals, as it requires accurate measures of the number of offspring produced per individual. This is especially difficult in species that occur at low densities and are difficult to observe and capture. Maternity can often be identified by the presence of the mother, however polygynous large mammals rarely provide paternal care. In such cases molecular techniques can be used to determine paternity (Clutton-Brock 1988; Clutton-Brock, Albon & Guinness 1988; Clapham & Palsboll 1997; Coltman, Bancroft, Robertson, Smith, Clutton-Brock & Pemberton 1999).

Due to the absence of paternal care in most mammals, male reproductive success is constrained only by the ability to sire offspring (Trivers 1972). Thus, male mammals usually compete intensely for mates, creating the potential for a high variance in male mating success (Emlen & Oring 1977), and thus an opportunity for sexual selection (Wade & Arnold 1980; Arnold & Wade 1984). Sexual selection, however, can only occur if variation in mating success is correlated with phenotypic variation (Andersson 1994). Sexual dimorphism and weaponry have most likely evolved as adaptations in species in which males compete for access to females (Andersson 1994).

Intrasexual selection favors traits that confer an advantage on males in gaining access to females (Andersson 1994). Large body size is one such trait, because of its advantage to males during combat and endurance rivalry (Andersson 1994). When male mating success is strongly influenced by fighting, sexual selection promotes sexual size dimorphism, with males larger than females. Therefore male reproductive success is then expected to be biased towards a few large adults with superior competitive abilities. Intersexual selection may also favor large male size, if females prefer large males (Anderson 1994). Body size has often been found to be a major contributing factor to male reproductive success (e.g. red deer, *Cervus elaphus*, Clutton-Brock, Guinness & Albon 1982; Clutton-Brock *et al.*, 1988; bridled nailtail wallaby, *Onychogalea fraenata*, Fisher & Lara 1999; common brushtail possum, *Trichosurus vulpecula*, Clinchy, Taylor, Zanette, Krebs & Jarman 2004), but exceptions have also been found (harbor seal, *Phoca vitulina*, Coltman, Bowen & Wright 1998; Coltman *et al.* 1999).

Body size and age are closely linked in many large mammals, and also age is often associated with male reproductive success (e.g. Clutton-Brock *et al.* 1982; 1988). Older males are often more experienced (East, Burke, Wilhelm, Greig & Hofer 2003) and more dominant (Clutton-Brock *et al.* 1988; LeBoeuf & Reiter 1988), and therefore superior competitors in male-male competition. Due to viability selection, older males may also be of higher genetic quality (Trivers 1972). However, younger males may use alternative mating strategies (e.g. Hogg 1984).

ARS may also be influenced by population density, and mating skew may either increase or decrease with density (Kokko & Rankin 2006). In an expanding population of brown bears, the relative population density of females declines more rapidly than for males from the center of the reproductive area towards the edge (Swenson, Sandegren, Bjärvall & Wabakken 1998a, Swenson, Sandegren & Söderberg 1998b), which may affect male ARS. In red deer, for example, the lifetime breeding success of males was positively correlated with the local density of females (Clutton-Brock *et al.* 1988).

From a genetic perspective, superior reproductive competitors may have greater multilocus heterozygosity, which is often correlated with fitness-associated traits (David 1998, Hansson & Westerberg 2002). Significant correlations between multilocus heterozygosity and fitness have been found in birds (Hansson, Bensch, Hasselquist & Åkeson 2001) and mammals (Coltman *et al.* 1998; Slate, Kruuk, Marshall, Pemberton & Clutton-Brock 2000). Brown (1997) suggested that the expression of vigor, condition-sensitive ornaments, and symmetry in males may be a direct reflection of individual heterozygosity at key loci or many loci.

Here we evaluate ARS and its determinants in male brown bears (*Ursus arctos*) through a genetic paternity analysis in a 17-year study of two bear populations in Sweden. The brown bear is thought to be a nonsocial and nonterritorial species, exhibiting a polygamous and promiscuous mating system, in which males compete for the access to individual estrous females (Schwartz, Miller & Haroldson 2003). The objectives of this study were to estimate the influence of phenotypic factors, age and population density on variation in ARS of male brown bears. We predict that, a) male body size, b) male age, and c) population density are positively correlated with male ARS, and that d) male internal relatedness (a measure of genetic heterozygosity; Amos, Worthington Wilmer & Kokko 2001) is negatively correlated with male ARS.

Methods

STUDY AREA AND FIELD METHODS

The study areas were in south-central Sweden (approximately 61° N, 14° E, southern study area) and northern Sweden (approximately 67° N, 18° E, northern study area). The rolling southern study area (south) consists of 13,000 km² of intensively managed boreal forest and contains a hunted bear population. The mountainous northern study area (north) encompasses 8,000 km² and includes mountainous national parks and adjacent forested lands. Bears are not legally hunted in the national parks. For a detailed description of the study areas see Zedrosser, Dahle & Swenson (in press).

We immobilized bears from a helicopter in April-May, shortly after den emergence. A tissue sample was taken for genetic analysis and, for bears of unknown age, a first premolar was extracted for age determination (Matson et al. 1993). The head circumference (maximum circumference at the zygomatic arches) was measured with a tape measure and used as a measure of overall size of a male. Head circumference was used because Derocher & Stirling (1998) suggested that head measurements rather than body length might provide the most useful measures to compare populations of polar bears (*Ursus maritimus*).

INDIVIDUAL POPULATION DENSITY INDEX AND SPATIAL DISTRIBUTION

In the southern study area a population size estimate, based on a DNA analysis of non-invasive sampling of scats, was carried out in 2001 and 2002 (Bellemain, Swenson, Tallmon, Brunberg & Taberlet 2005). Following the procedures described by Zedrosser et al. (in press) we calculated an individual density index (within a radius of 17.84 km) around each radio marked individual in our analysis, which corresponds to the density of bears per 1000 km². The procedures used by Zedrosser et al. (in press) are based on the location of individuals genetically identified by the scat sampling, the location of the radiomarked bears (71% of the radio marked bears were represented in the genetic samples from scats (Bellemain *et al.* 2005)), and the growth rate in the population (used to temporally correct the density estimate throughout the study period).

In the northern study area virtually every adult male and female and all subadult female bears were radio-marked from 1995 to 2002 (Swenson, Sandegren, Brunberg & Segerström 2001). Following the procedures described in Zedrosser et al. (in press) we used these data and data on growth rate of the population to calculate an individual density index like in the southern study area. Although based on different methods, we regard the indices of both study areas as comparable, because we are confident that virtually all individuals (except subadult males,

which were accounted for) were radiomarked in the northern study area, and the density estimates based on the genetic sampling in the south was corrected by dividing it by the proportion of radiomarked bears identified in the genetic sample. The average population density index was 11.1 bears/1000km² in the north and 29.3 bears/1000km² in the south (Støen, Zedrosser, Sæbø & Swenson, in press).

To ensure that estimates of male ARS were not affected by changes in spatial distribution of adult males over time, we compared mean and median home range diameters and the mean distance between adult male brown bear annual home range centers in our study areas. If adult males commonly shift their home ranges between years, mean distances between annual home range centers should be large in relation to the mean home range diameters. The mean and median home range diameters, based on 95% minimum convex polygon home ranges, had been published previously by Dahle & Swenson (2003). The mean distance between adult male brown bear annual home range centers were calculated based on radio-telemetry locations and 95% minimum convex polygon home ranges.

PATERNITY ANALYSIS, DATA SELECTION AND INTERNAL RELATEDNESS

Eighteen microsatellite loci, described in Paetkau & Strobeck (1994) and Taberlet, Camarra, Griffin, Uhrès, Hanotte, Waits, Dubois-Pagnon, Burke & Bouvet (1997), were amplified using Polymerase Chain Reaction. The amplification and analysis of microsatellites was carried out following the protocol described in Waits, Taberlet, Swenson, Sandegren & Franzén (2000). Our database consisted of 738 multilocus genotypes, including radio-marked and hunter-killed individuals.

We estimated ARS for each individual male as the genetically detected number of offspring surviving to 1 year of age per year. For most of the offspring used in this analysis, the mother was known, because yearlings were captured while accompanying their mother. For bears with unknown pedigree, we determined parentage using the software PARENTE (Cercueil, Bellemain & Manel 2003). Paternity probabilities were calculated using the same software, taking into account the allelic frequencies, global error rate and sampling rate of the population (Cercueil *et al.* 2003). One allelic incompatibility of 18 loci was allowed in the comparison of the father-offspring genotype in order to consider the 0.8% error rate in the genetic data set (Bonin, Bellemain, Bronken Eidesen, Pompanon, Brochmann & Taberlet 2004).

Using 18 polymorphic markers to assign parents to the offspring, the probabilities of identity, i.e. the probability to obtain two identical genotypes, from two different individuals by chance (PI, Paetkau & Strobeck (1994); PIsib, for siblings, Waits *et al.* (2001)) was very low:

PI=3.1 10⁻¹⁷ and PIsib=2.4 10⁻⁷. In addition we considered only fathers that were geographically possible and had a high probability of paternity (P>0.75), which helped to prevent incorrect paternity assignments and artefactual relationships between heterozygosity and paternity assignment.

For all individuals participating used in this study, we calculated an internal relatedness index (IR). This IR-index reflects a quantity measured between parental half-genotypes. It is an estimator of heterozygosity, giving more weight to homozygotes involving rare alleles and reflects parental similarity better than commonly used heterozygosity indices (Amos *et al.* 2001). It is calculated as:

$$IR = \frac{2H - \sum f_i}{2N - \sum f_i} \text{ (Amos } et al. \text{ 2001),}$$

where H represents the number of homozygous loci within an individual; N the number of loci genotyped and f_i the frequency of the i th allele contained in the genotype.

STATISTICAL ANALYSES

To estimate absolute size in the years a male was not captured, we calculated the von Bertalanffy growth curve (von Bertalanffy 1938) for each study population. The average deviation in size of an individual from the mean population growth curve was used to calculate an individual growth curve, from which we derived absolute body size at a given age. Because all bears were captured within a 2-week period in each study area, we did not adjust body size for capture date. The von Bertalanffy curve was used for growth curve analysis, because it has been used previously to describe the growth of bears (Kingsley, Nagy & Reynolds 1988, Derocher & Stirling 1998, Zedrosser *et al.*, in press). The von Bertalanffy size-at-age equation was used in the form

$$s_a = S(1 - e^{-k(a-A)})^3$$

where s_a = head circumference (cm) at age a , S = asymptotic head circumference (cm), k = size growth rate constant (years⁻¹), A = fitting constant (extrapolated age at zero size) (years). Several individuals have been captured more than once during our study period; we used only the measurement taken at the highest age in our analysis.

Differences in male age structure, male ARS and proportion of successful males per age class between study areas were tested using independent samples t -tests. To examine the relationship between ARS success and several categorical and covariate factors, while controlling for dependences in the data set, we used general linear mixed models (GLMM). We first analyzed the whole dataset (global GLMM) before analyzing each area separately

(GLMM). We assumed a Poisson data distribution and composed global models that accounted for the effects of multiple explanatory variables on ARS. Overdispersion in our data set was handled by using random effects, which is a way of modeling overdispersion in Poisson models (McCulloch & Searle 2001). The least significant terms were excluded in a backward stepwise manner until the final model consisted of only significant ($P < 0.05$) or suggestive terms ($P < 0.1$). We used the statistical software R 1.9.0 (R Development Core Team 2004, <http://www.R-project.org>) in all analyses.

Results

Genetic information about ARS was obtained for males that were captured from 1984-2001. We obtained reproductive data from 68 males (24 in the north, 44 in the south) for 417 mating seasons (the number of matings seasons the males in our sample were alive). The spatial distribution of males was stable over time, because the mean distance between male annual home range centers was shorter than both the mean and median home range diameters of adult males in both study areas (Table 1). Male age ranged from 3-30 years, and ages of successful males ranged from 3-27 years. The male age structure differed between the study areas (Fig. 1); the mean male age was significantly higher in the south than in the north (South: $\bar{X} = 9.55$ years ± 5.93 (SD), North: $\bar{X} = 6.88$ years ± 4.51 , $t_{58} = 2.08$, $P = 0.042$). Mean ARS was significantly higher in the north than in the south (North: $\bar{X} = 1.02$ genetically detected offspring per year ± 1.59 , South: $\bar{X} = 0.42$ genetically detected offspring per year ± 0.95 , $t_{134} = 3.69$, $P < 0.001$; Fig. 2). There was also a statistically significant difference in the proportion of males per age class that were reproductively successful between the study areas (South: age classes 3-30, $\bar{X} = 21.4$ % ± 32.6 , North: age classes: 3-24, $\bar{X} = 56.8$ % ± 42.1 , $t_{38} = 2.56$, $P = 0.014$, Fig. 3).

The von Bertalanffy curves (based on 74 individuals in the north and 152 in the south) were not significantly different between the study areas (Table 2, Fig. 4). We used the study-area specific growth curves to calculate the body size of the individuals used in the further analyses. The overall model of both study areas explaining the detected number of offspring produced by a male brown bear showed that male ARS was significantly lower in the south (Table 3). Age and population density were positively related, and internal relatedness was negatively related to male ARS. The interaction study area*body size suggested that body size was more important in the south, whereas the interaction study area*age showed that age was more important in the north (Table 3). The separate analysis of the study areas showed that the detected number of offspring produced per year by a male brown bear was significantly related to age and

population density in the north, and significantly related to body size and suggestively related to population density in the south (Table 4).

Discussion

ARS is a measurement of an individual's short-term (seasonal) production of offspring. In general, measures of ARS in this study might be underestimates, because males could have sired offspring outside the study area or produced young within the study area that were not detected. Bear hunting in Scandinavia is random in the sense that no age or sex classes, except females with accompanying young, are protected and hunters show little selection (Fujita 2000). Age patterns or spatial organization in natural, non-hunted brown bear populations and the importance of some factors influencing male ARS may differ between unhunted and hunted populations. Our measures of ARS are from hunted (legally and illegally) populations.

We found a significant difference in male ARS between the study areas, with males producing fewer offspring annually in the south (Table 3, Fig. 2). This was probably due to a lower operational sex ratio in the south (more adult males per adult female; Swenson *et al.* 2001, Swenson 2003). Due to illegal killing, especially in the spring, the male bear population in the north consisted of one old and reproductively dominant male and several young adult males for several years (Swenson *et al.* 2001). Males 9 years were largely missing (Fig. 1). This uneven distribution of age classes apparently enabled a higher proportion of the relatively more common young males (3-4 years) to gain reproductive success in the north than in the south (Fig. 3). These young males also achieved higher ARS in the north than in the south (Fig. 2). In the south bears are usually killed during a regulated autumn hunting season. This resulted in a more evenly distributed male age structure and an increasing ARS with age classes (Fig. 1, Fig. 2).

Generally, ARS was positively correlated with age. We found no evidence of reproductive senescence in male brown bears, as occurs in male red deer (Clutton-Brock *et al.* 1988) and female brown bears (Schwartz, Keating, Reynolds, Barnes, Sellers, Swenson, Miller, McLellan, Keay, McCann, Gibeau, Wakkinen, Mace, Kasworm, Smith & Herrero 2003), because all males over 20 years reproduced regularly. Females of many species choose to mate with old rather than young males, possibly because older males pass superior genes on to their offspring (Brooks & Kemp 2001). Age in males may reflect their genetic quality (the viability selection hypothesis, Trivers 1972), and/or those males may also be more selected by females (the good gene hypothesis, Brown 1997). However this latter hypothesis (Brown 1997) may not be applicable to our study, because both of our study populations were under heavy hunting

pressure and therefore bear survival may not depend on genetic quality. Additionally the mortality rates of adult bears (> 3 years) are independent of age (Sæther, Engen, Swenson, Bakke & Sandegren 1997). Older males may show a higher reproductive effort, as in reindeer (*Rangifer tarandus*) (Mysterud, Holand, Røed, Gjøstein, Kumpula & Nieminen 2003), or they may be more experienced and efficient in the scramble competition for females.

Several studies show that male age is often strongly correlated with rank (Clutton-Brock *et al.* 1982; 1988; Le Boeuf & Reiter 1988; Coltman, Festa-Bianchet, Jorgenson & Strobeck 2001), however all of these studies dealt with species with temporary harem polygyny. Brown bears are considered to be a nonsocial species, however a spatial male dominance hierarchy based on age and size cannot be excluded, as suggested for brown bears at garbage dumps (Craighead, Sumner & Mitchell 1995), and for American black bears (*Ursus americanus*) (Kovach & Powell 2003) and polar bears (Derocher & Stirling 1990).

The mating system of brown bears is based on male contest competition for females (Schwartz *et al.* 2003a), which is also indicated by the large sexual size dimorphism (Anderson 1994). As predicted, male body size (corrected for age) was positively correlated with ARS. This suggests that larger males are able to physically dominate and exclude smaller males when competing for estrous females, as has been found in several studies on other species (Clutton-Brock *et al.* 1988; LeBoeuf & Reiter 1988; McElligott, Gammell, Harty, Paini, Murphy, Walsh & Hayden 2001; Wilson *et al.* 2002). An alternative explanation may be that larger males are more often selected by females, as has already been suggested for brown bears (Bellemain *et al.* 2006). A certain advantage of body size in endurance competition may also be involved. In general, the capacity for energy storage should increase with body size more rapidly than metabolic costs (Andersson 1994). Large size and stored energy in form of fat may enable a male to roam wider and longer in search of females. In bighorn sheep (*Ovis canadensis*) younger or subdominant males that were not able to tend an estrous female employed mating tactics like cursing and blocking relatively more often than adult males, which successfully tended estrous females (Hogg 1984). However, to our knowledge, no alternative mating tactics of younger or smaller males have been observed in brown bears.

The separate analyses of the study areas and the interactions of study area*age and study area*body size suggest that age was more important for ARS in the north and body size was more important in the south. Body size and age of male brown bears are highly correlated in our study areas (Bellemain *et al.* 2006). The study area differences in the importance of body size and age are likely related to the aforementioned differences in male age structure due to human influence in the study areas. A single old male dominated the reproduction in the north during

the study period (Fig. 2), and this most likely resulted in the relatively higher importance of age in the north. In the south, the area with the more even male age structure, no single male was able to dominate. This most likely resulted in a more intense competition among males, with body size as the deciding factor.

As predicted, population density had a positive effect on the number of offspring produced per male. The Scandinavian bear population is expanding in size and range (Swenson, Wabakken, Sandegren, Bjärvall, Franzén & Söderberg 1995), and Swenson *et al.* (1998a,b) showed that the relative density of females declined more rapidly than for males from the center of the reproductive area towards the edge and that low-density areas into which bears are expanding were dominated by males. The declining female density towards the population edge decreases the chances for males to obtain mating opportunities and therefore also their ARS.

As predicted, IR was negatively correlated with ARS. Negative values are suggestive of relatively outbred individuals, whereas high positive values suggest inbreeding. The negative correlation in our results suggests that outbred individuals have a higher ARS. The reason why IR was not significantly correlated with male ARS when the study areas were analyzed separately was most likely related to sample size, because the effects of measures of heterozygosity typically are only evident with large sample sizes (David 1998). Individual heterozygosity at key or many loci may be reflected in male physical qualities and condition-sensitive traits (Brown 1997). Some of these traits may directly benefit males in competition. However, heterozygosity may also be selected via female choice; a female might choose the most heterozygous male through physical cues because it may favor the production of diverse and superior offspring. In brown bears, females seem to select genetically diverse males for mating (Bellemain *et al.* 2006). This has also been suggested in gray seals (*Halichoerus grypus*) (Amos *et al.* 2001), and in red deer lifetime breeding success for both males and females was positively correlated with heterozygosity (Slate *et al.* 2000). Less inbred, and thus more heterozygous males, may also have an advantage in sperm competition (Andersson 1994). Internal relatedness as a measure of heterozygosity is probably reflected by male quality due to the functional overdominance hypothesis (Bellemain *et al.* 2006).

In conclusion, the male population structure and the patterns of ARS varied between the study areas, partly due to human influence. Older and larger males had a higher ARS, but age was relatively more important in the north and body size was more important in the south. Both variables are often correlated in mammals, and are related to advantages in dominance and contest-competition. IR, reflecting multilocus heterozygosity, was important for male ARS. Individual heterozygosity may be reflected in male qualities, which may be of benefit in direct

male-male competition, in sperm competition, or female mate selection. Population density was also positively correlated with male ARS, which may be related to the structure of an increasing bear population, with female densities declining towards the population edge.

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1 **Table 1.** Comparison of mean and median home range diameters and the mean distance
 2 between adult male brown bear annual home range centers in two study areas in Scandinavia
 3 in the period 1984-2001. Males were aged 3-30 years (North: 22 males with radio-locations
 4 from together 74 years; South: 34 different males with radio-locations from together 126
 5 years). Home range sizes are in km², the distances calculated are in km. Median diameter =
 6 median home range diameter as calculated from the median home range. Mean diameter =
 7 mean home range diameter as calculated from the mean home range. Mean distance = the
 8 mean distance between male annual home range centers between subsequent years.

9

Study area	Median home range	Mean home range	Range	Median diameter	Mean diameter	Mean distance
North	833 km ² *	1137 km ² *	245-2029 km ² *	16.28 km	19.02 km	12.7 km**
South	1055 km ² *	4289 km ² *	314-8264 km ² *	18.33 km	36.95 km	11.6 km**

10

11 * data from Dahle & Swenson (2003), based on 95% minimum convex polygon home ranges

12 ** based on radio-telemetry locations and 95% minimum convex polygon home ranges

13 **Table 2.** Parameter estimates for the von Bertalanffy size-at-age curves for head
14 circumference of male Scandinavian brown bears ($\pm SE$) in two study areas in Scandinavia. S
15 is the asymptotic head circumference, K is the size growth constant, A is the theoretical age at
16 which the animal would have size zero, and N is the sample size.

17

Study area	S (cm)	K (year ⁻¹)	A (years)	N
North	78.28 \pm 1.81	0.384 \pm 0.047	-3.25 \pm 0.48	74
South	77.68 \pm 0.80	0.335 \pm 0.018	-3.83 \pm 0.24	152

18

19 **Table 3.** A global generalized mixed linear model explaining the detected number of
 20 offspring produced annually by a male brown bear in two study areas in Scandinavia in the
 21 period 1984-2001. Variables included are study area, age, body size, internal relatedness,
 22 density and relevant interactions. Male identity was included as a random effect. After a
 23 successive exclusion of the least significant terms, the final model is shown in the table. *Df* is
 24 degrees of freedom, β is the logistic regression coefficient, *SE* is the standard error, *t* denotes
 25 the t-value and *P* denotes the significance level. N=417, number of individuals: 68.
 26

Explanatory variables	<i>df</i>	β	<i>SE</i>	<i>t</i>	<i>P</i>
Study area	66			-2.284	0.026
South		-6.086	2.665		
North		0	0		
Age	343	0.079	0.040	1.988	0.048
Body size	343	-0.008	0.029	-0.272	0.786
Internal relatedness	343	-1.869	0.798	-2.343	0.020
Density	343	0.016	0.007	2.322	0.021
Study area*body size	343			1.954	0.051
South*body size		0.079	0.041		
North*body size		0	0		
Study area*age	343			-2.007	0.046
South*age		-0.104	0.052		
North*age		0	0		

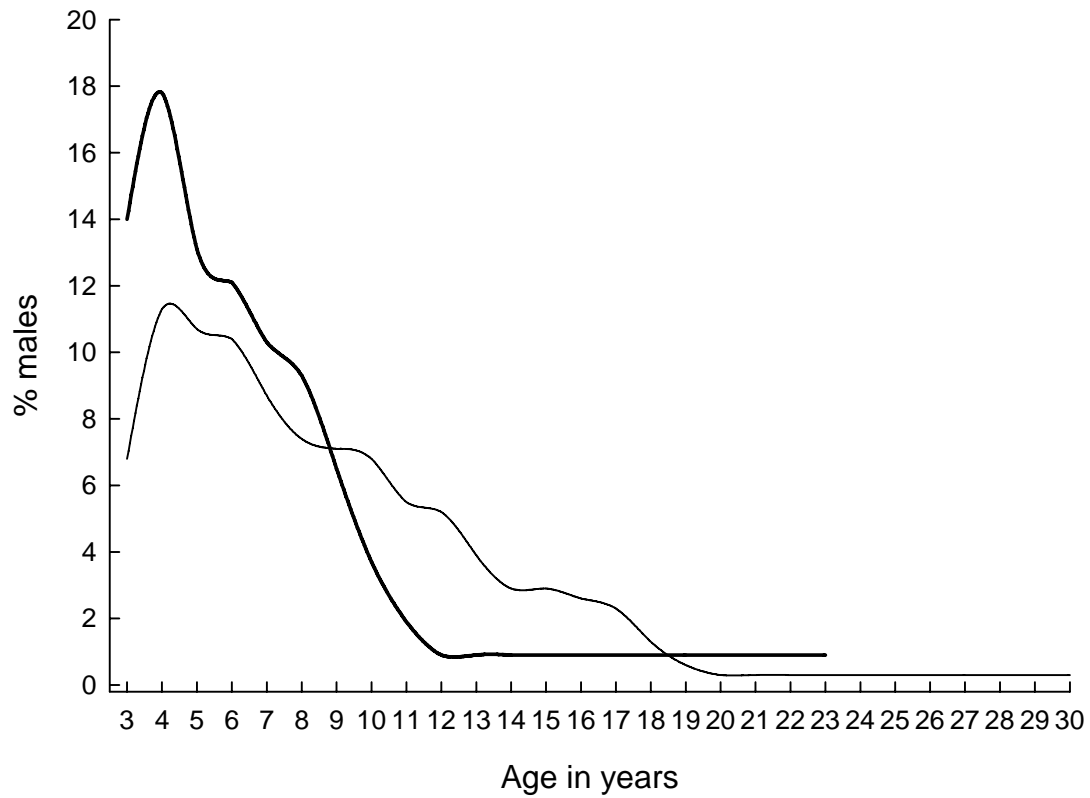
27

28 **Table 4.** Separate generalized mixed linear models explaining the detected number of
 29 offspring produced annually by a male brown bear in two study areas in Scandinavia in the
 30 period 1984-2001. Variables included are age, body size, internal relatedness, population
 31 density and relevant interactions. Male identity was included as a random effect. After a
 32 successive exclusion of the least significant terms, the final models are shown in the table. *Df*
 33 is degrees of freedom, β is the logistic regression coefficient, *SE* is the standard error, *t*
 34 denotes the t-value and *P* denotes the significance level. Northern study area: N = 108,
 35 number of individuals = 24. Southern study area: N = 309, number of individuals = 44.
 36

Study area	Explanatory variables	<i>df</i>	β	<i>SE</i>	<i>t</i>	<i>P</i>
North						
	Age	82	0.063	0.024	2.632	0.010
	Population density	82	0.039	0.016	2.399	0.019
South						
	Body size	263	0.063	0.022	2.841	0.005
	Population density	263	0.014	0.008	1.826	0.069

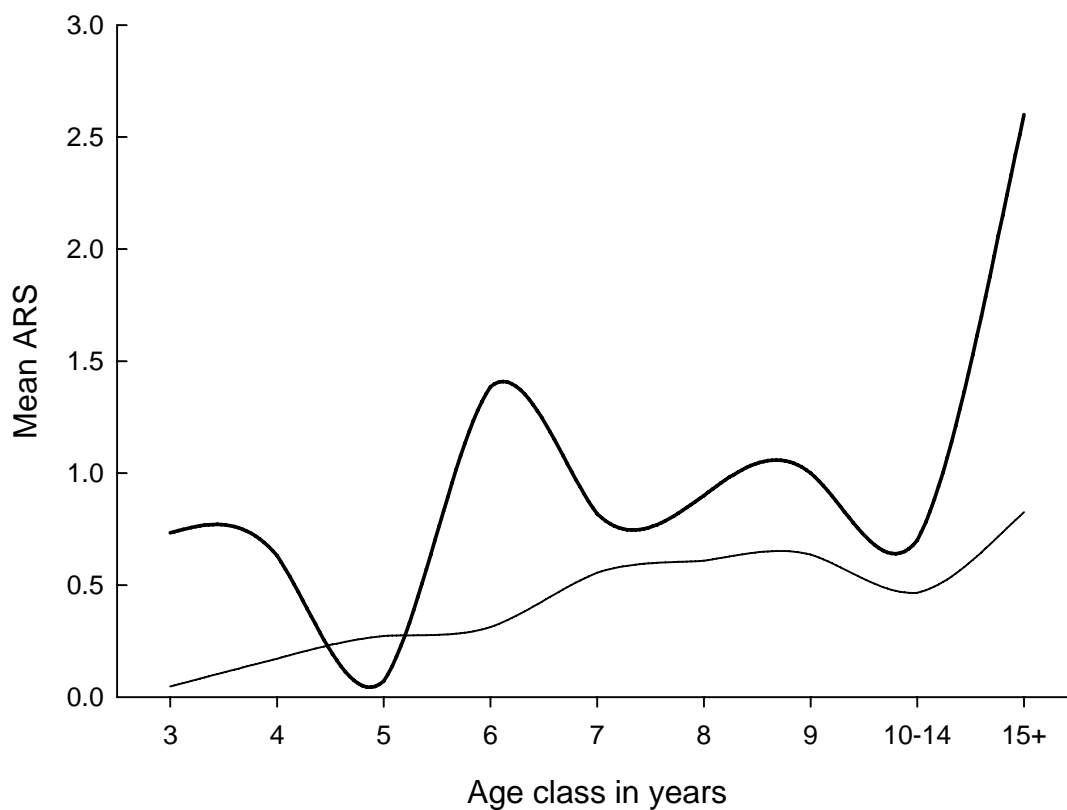
37

38 **Fig. 1.** Percentage of adult (≥ 3 years) male brown bears in two study areas in Scandinavia
39 from 1984-2001. The thick solid line represents males in the northern study area and the thin
40 solid line males in the southern study area.



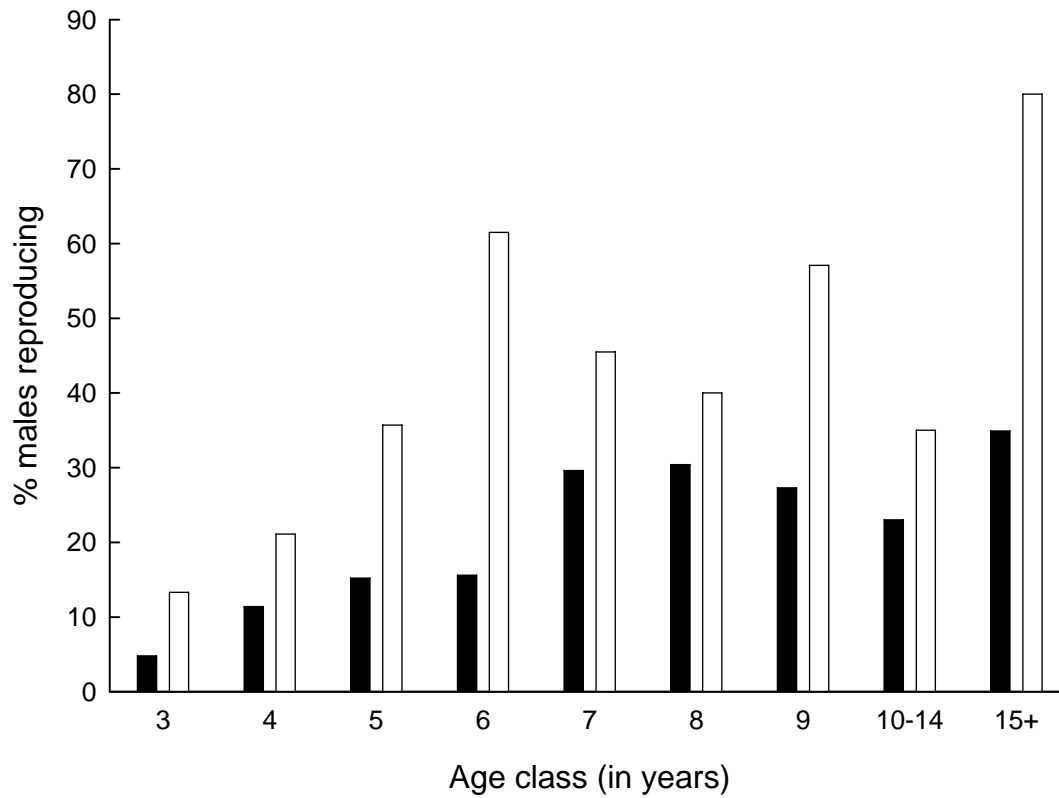
41

42 **Fig. 2.** Distribution of mean annual reproductive success (ARS) among age classes in male
43 brown bears in two study areas in Scandinavia from 1984-2001. ARS was estimated as the
44 genetically detected number of offspring per year surviving to 1 year of age. The thick solid
45 line represents males in the northern study area and the thin solid line males in the southern
46 study area.



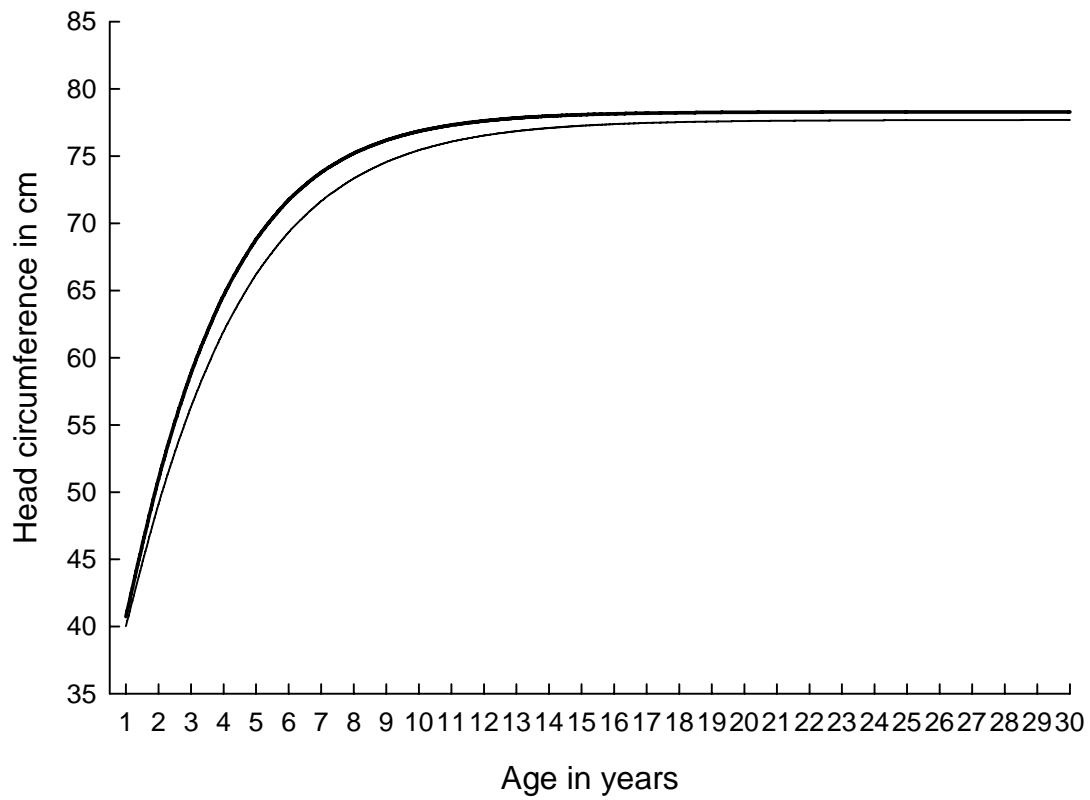
47

48 **Fig. 3.** Percentage of adult (≥ 3 years) male brown bears reproducing annually per age class
49 in two study areas in Scandinavia from 1984-2001. The black bars represent the southern
50 study area, the white bars the northern study area.



51

52 **Fig. 4.** The von Bertalanffy growth curve fitted to age and head circumference of male
53 Scandinavian brown bears. The thick solid line represents males in the northern study area
54 and the thin solid line males in the southern study area.



55