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, Arnbom et al. 1997). Offspring of larger mothers may also show increased pre-weaning growth (Myers and Master 1983, Arnbom 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) (Hrdy 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 (*Oncorhyncus* 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 matrilineal 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 km^2 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 km^2 of mountainous national parks and adjacent forested land about 100 km north of the arctic circle. The area is characterized by deep valleys, glaciers and high plateaus ranging up to 2,000m. 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 peretinoal 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 nämden 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 = $3.10x10^{-17}$ and Pisib = $3.10x10^{-7}$) (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 km^2. 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 ($\overline{X} = 24.5 \pm 0.5$ (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*), Arnbom 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 beenreported, 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: one 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 chose 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 (Maestripieri 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. Maestripieri 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 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

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 ($\overline{X}$ = 24.5 ± 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*

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, 1998*a*). It is important to understand the variation in body mass, because it may have a pronounced effect on survival and reproductive success.

In this paper we analyse 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, Bijnens & Dhondt, 1993; Arnbom, Fedak & Boyd, 1997) and offspring of larger mothers may show increased pre-weaning growth (Myers & Master, 1983; Arnbom *et al*., 1997; Barbraud *et al*., 1999). Most studies have used maternal mass as the maternal trait (e.g. Derocher & Stirling, 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; Sydeman *et al*., 1991; Hewison & Gaillard, 2001). Reproductive senescence has been reported for female brown bears (Schwartz *et al*., 2003), but possible relationships between maternal age and other reproductive parameters have not been reported in brown bears. Derocher & Stirling (1994) found that litter mass and litter size in polar bears followed a curvilinear relationship with maternal age, and Derocher 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,

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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, 2001*a*). Availability of berries varies among years in the boreal forest as does brown bear food habits (Nilsen, 2002). For this reason we predicted (8) that body size and mass of yearlings should differ among cohorts (Table 1).

Life history effects of size and mass

To evaluate the life-history effect of size and mass, we also analysed juvenile survival. Early survival (Winters *et al.*, 1947; Haukioja & Salovaara, 1978; Baker & Fowler, 1992; Derocher & Stirling, 1996) and survival to adulthood (Albon *et al*., 1987; Festa Bianchet *et al*., 1997) 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 km^2 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 km^2 of mountainous national parks and adjacent forested land about 100 km north of the Arctic Circle. The area is characterized by deep valleys, glaciers and high plateaus ranging up to 2.000m. 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 km^2) 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) 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 Δ *AIC_c* < 2 should

receive consideration in making inferences (Burnham & Anderson, 1998). The within litter variation in size and mass of yearlings was analysed with paired t-tests. Two-tailed tests were used, and an α level of 0.05 was selected for statistical significance. S PLUS v. 6.2 (Insightful Corp., Seattle, WA, USA) was used in all statistical analyses. Mean values are presented with standard errors (SE).

Mortality of cubs-of-the-year was higher in the south than in the north, but in both areas most of the mortality took place during the mating season in May-June (Swenson *et al.*, 1997; 2001*b*), before the lactation peak during summer (Farley & Robbins, 1995). For this reason statistical analyses were carried out twice, using 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 ($\overline{\mathrm{X}}$ = 24.5 ± 0.5), and head circumference varied from 33 to 48 cm ($\overline{\mathrm{X}}$ = 40.3 ± 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: β = 1.988 ± 1.025, df = 145, t = 1.940, P = 0.054; mass: β = 4.882 ± 2.096, df = 143, t = 2.329, P = 0.021), which decreased in strength with increasing maternal size (size: β = -0.033 ± 0.017, df = 145, t = -1.970, P = 0.051; mass: β = -0.083 ± 0.034, df = 143, t = -2.417, P = 0.017), however these models had ΔAIC_c values of 10.3 and 3.8, for yearling size and mass, respectively. Models including the second order term of maternal age

(suggesting nonlinear relationships between maternal age and yearling size and mass) had ΔAIC_c 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 ($\overline{X}$ = 27.9 ± 1.2 kg) was on average 2.8 ± 0.4 kg heavier than the lightest yearling ($\overline{X}$ = 25.2 ± 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, $\overline{X}$ = 3.1 ± 0.8 kg, n = 12, female littermates, $\overline{X}$ = 1.9 ± 1 kg, n = 10, or mixed sex, $\overline{X}$ = 3.0 ± 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 (χ^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 ΔAIC_c values > 12 and 7 for body size and mass respectively. However, there was more support for a stronger

negative effect of population density on yearling mass in the southern study area than in the northern study area (t = 2.021, df = 144, p = 0.045, ΔAIC_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 (β = 0.311 ± 0.128, N = 120, P = 0.009, Table 1), but body mass seemed to have a weaker effect on survival (β = 0.089 ± 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,* Arnbom *et al*., 1997, roe deer, Andersen *et al*., 2000).

Surprisingly, the predicted relationship (2) between maternal age and offspring size was weak (judged from the high ΔAIC_c values of models including this term). The most likely explanation is that our sample included only 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 disproportionally 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 predenning black bear cubs-of-the-year were on average 40% heavier in years with abundant food than in years of scarcity. Brown bears, which are typical capital breeders, largely rely on stored adipose tissue for reproduction. Thus, early maternal expenditure is dependent on the food availability during summer and especially the fall, when pregnant females add adipose tissue and muscles 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 ± one standard error.

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

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

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

[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.*]
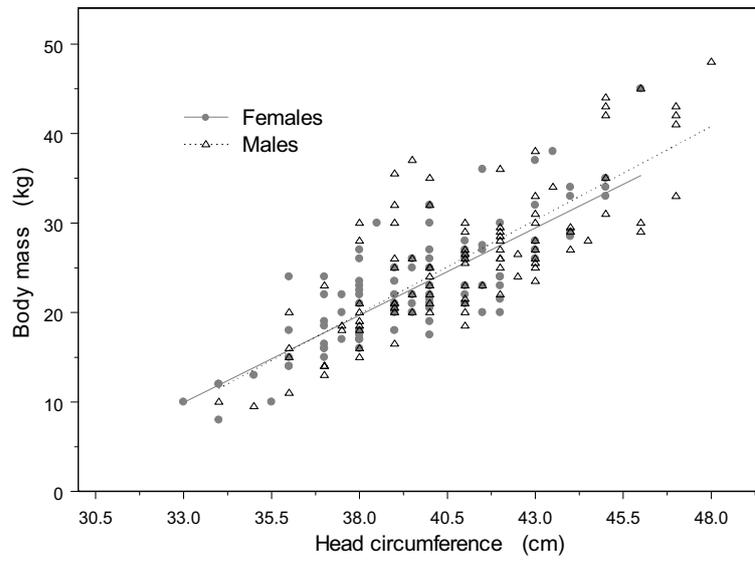
Paper II

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 km^2 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 pubsecens*), silver birch (*Betula pendula*), European aspen (*Populus tremula*) and gray alder (*Alnus incana*) are common. The elevations range from about 200 m in the southeastern part to about 1,000 m in the western part, but only a minority of the area is above timberline, which is about 750 m 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 km^2 of mountainous national parks and adjacent forested land about 100 km north of the arctic circle. The area is characterized by deep valleys, glaciers and high plateaus ranging up to 2,000m. 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 nämden i Uppsala).

Individual population density index, northern study area.—From 1995 to 2002 virtually every adult male and female and all subadult female bears were 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 km^2 commonly used as the basis of density measure for bears (McLellan 1994); the median adult male home range was 833 km^2 in this area (Dahle and Swenson 2003). The number of cubs present per adult female was estimated by dividing the mean litter size in our northern study area (2.4; Swenson et al. 2001) by the mean litter interval (2.6 years; Swenson et al. 2001), which resulted in an estimated 0.92 cubs present per adult female per year. Because no radiomarked subadult males were represented in the initial count of bears surrounding a given individual, we multiplied the number of subadult females by 2, assuming an even sex-ratio (Bellemain et al. 2005). The individual density index I_d in a radius of 17.84 km was calculated as $I_d = N_{ad.m} + 1.92N_{ad.f} + 2N_{subad.f}$, where $N_{ad.m}$ is the number of 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 km^2.

The Scandinavian brown bear population has expanded in size and distribution (Swenson et al. 1995). Sæther et al. (1998) reported a population growth rate of 14% annually in the northern study area in the period 1985-1994. The numbers of marked animals remained similar throughout the time period 1995-2002, despite a high and comparable capture effort in all years, suggesting stable densities. The temporally 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 km^2 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 km^2.

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

1993-2001. To temporally correct the individual population density indices for this period, we assumed stable densities from 1993-2002. 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 eyars 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 van 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 Δ *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 ($\overline{X}$ = 57.3 cm ± 3.2 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 (β = 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.

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 (*Callorbinus 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 km^2) than in the north (~11 bears/1000 km^2). 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 patters 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 (± *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 ± 0.69	0.368 ± 0.038	-4.01 ± 0.49	68
South	62.62 ± 0.49	0.445 ± 0.034	-3.47 ± 0.33	115

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

Fig. 1.
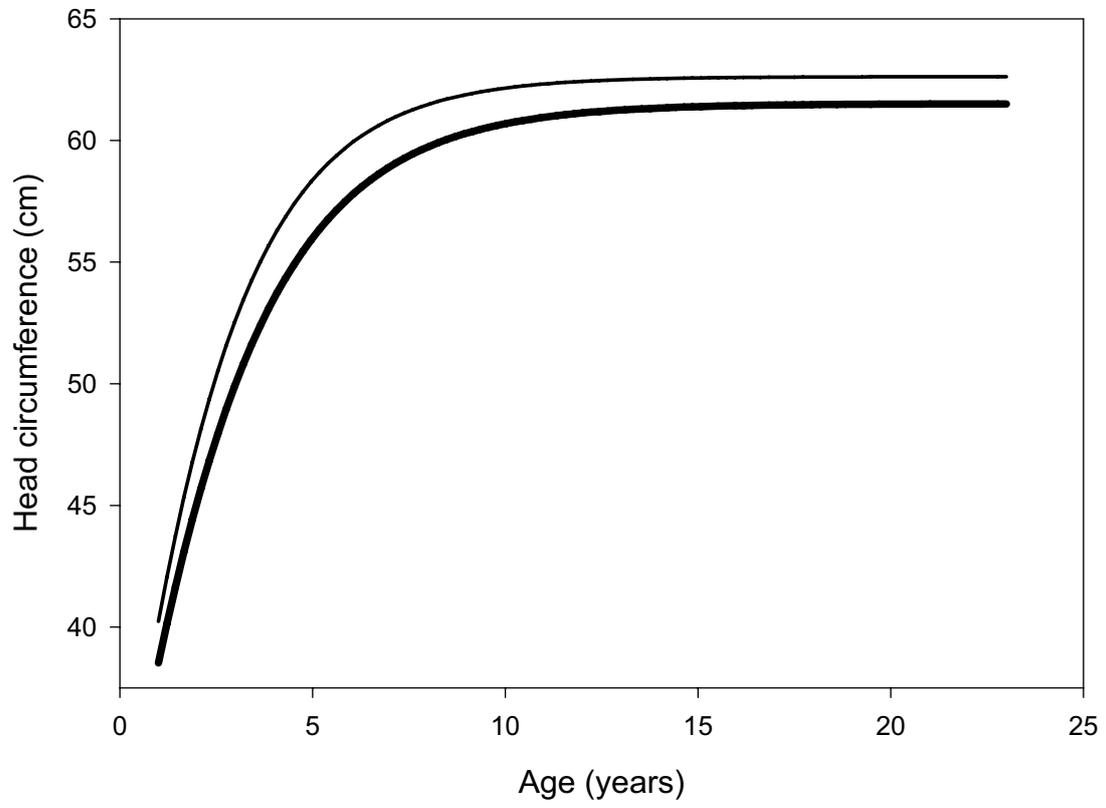
Paper III

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.

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, Guiness & Albon 1982; Clutton-Brock *et al.,* 1988; bridled nailtail wallaby, *Onochyogalea 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 & Wabakken1998a, 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 km^2 of intensively managed boreal forest and contains a hunted bear population. The mountainous northern study area (north) encompasses 8,000 km^2 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 km^2. 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:

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

where *H* represents the number of homozygous loci within an individual; *N* the number of loci genotyped and *fi* 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 ($P \leq 0.05$) or suggestive terms ($P \leq 0.1$). 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: $\overline{X} = 9.55$ years ± 5.93 (*SD*), North: $\overline{X} = 6.88$ years ± 4.51, $t_{58} = 2.08$, $P = 0.042$). Mean ARS was significantly higher in the north than in the south (North: $\overline{X} = 1.02$ genetically detected offspring per year ± 1.59, South: $\overline{X} = 0.42$ 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, $\overline{X} = 21.4$ % ± 32.6, North: age classes: 3-24, $\overline{X} = 56.8\% \pm 42.1$, $t_{38} = 2.56$, $P = 0.014$, 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 km^2, 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 (± *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 ± 1·81	0·384 ± 0·047	-3·25 ± 0·48	74
South	77·68 ± 0·80	0·335 ± 0·018	-3·83 ± 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	*df*	β	*SE*	*t*	*P*
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	*df*	β	*SE*	*t*	*P*
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.
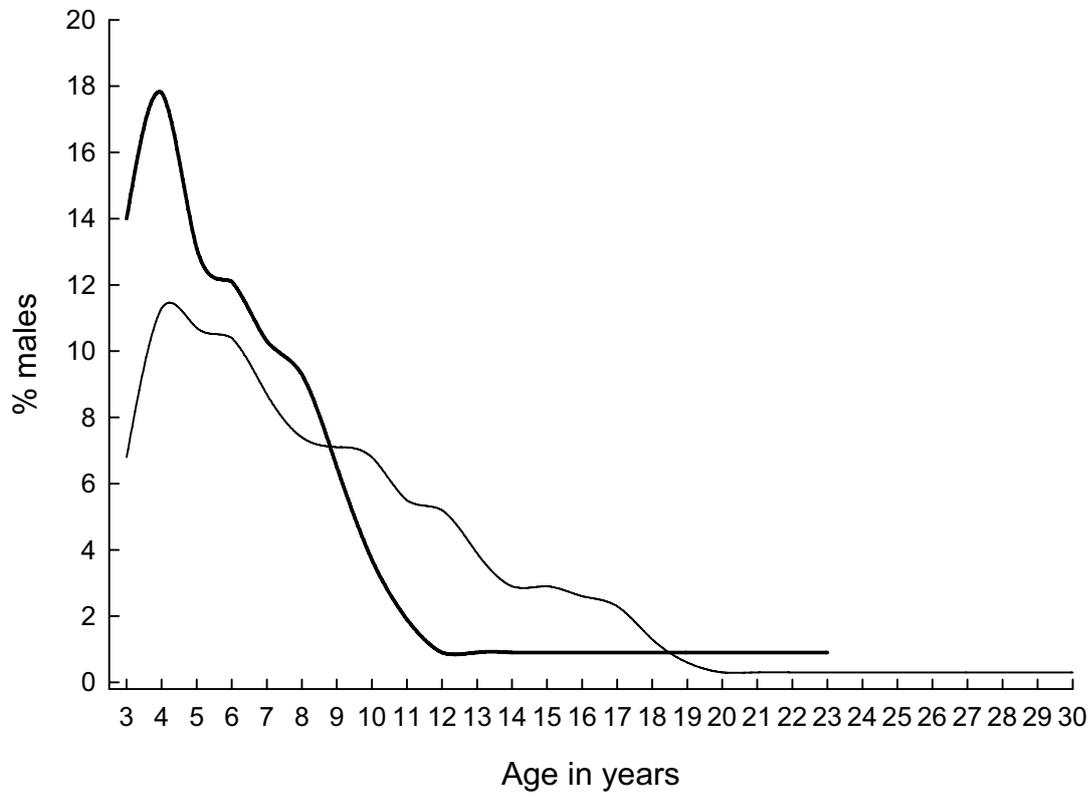
41

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.
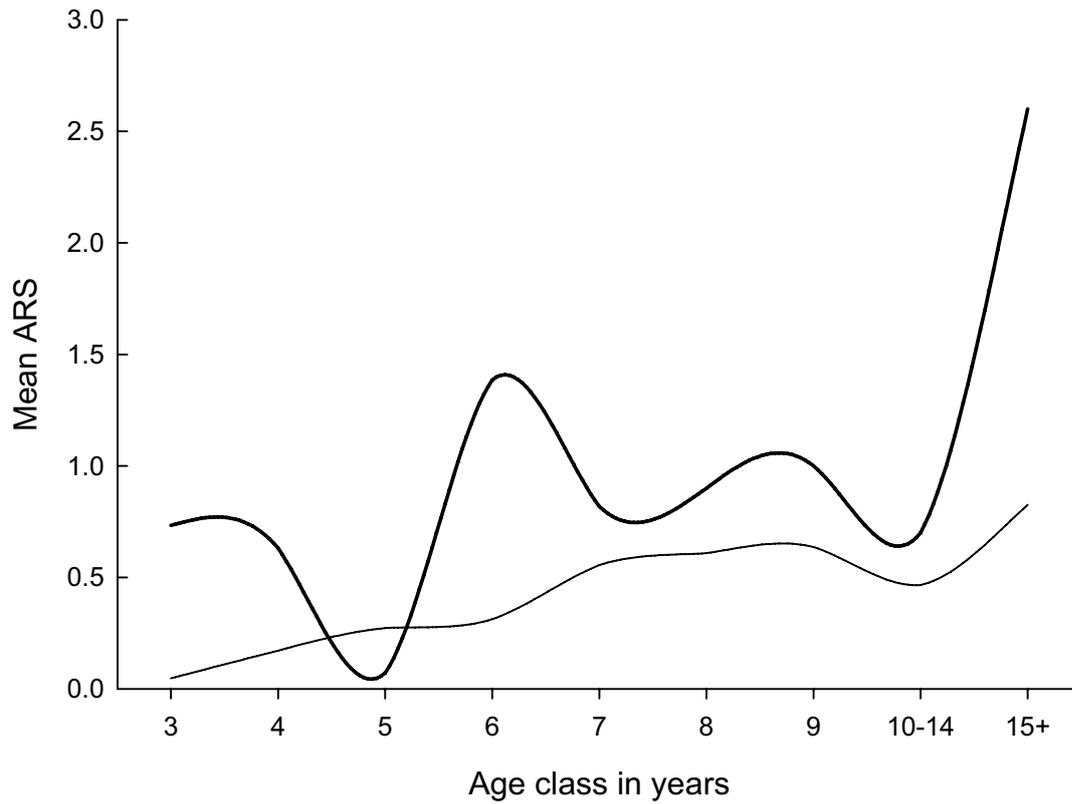
47

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.
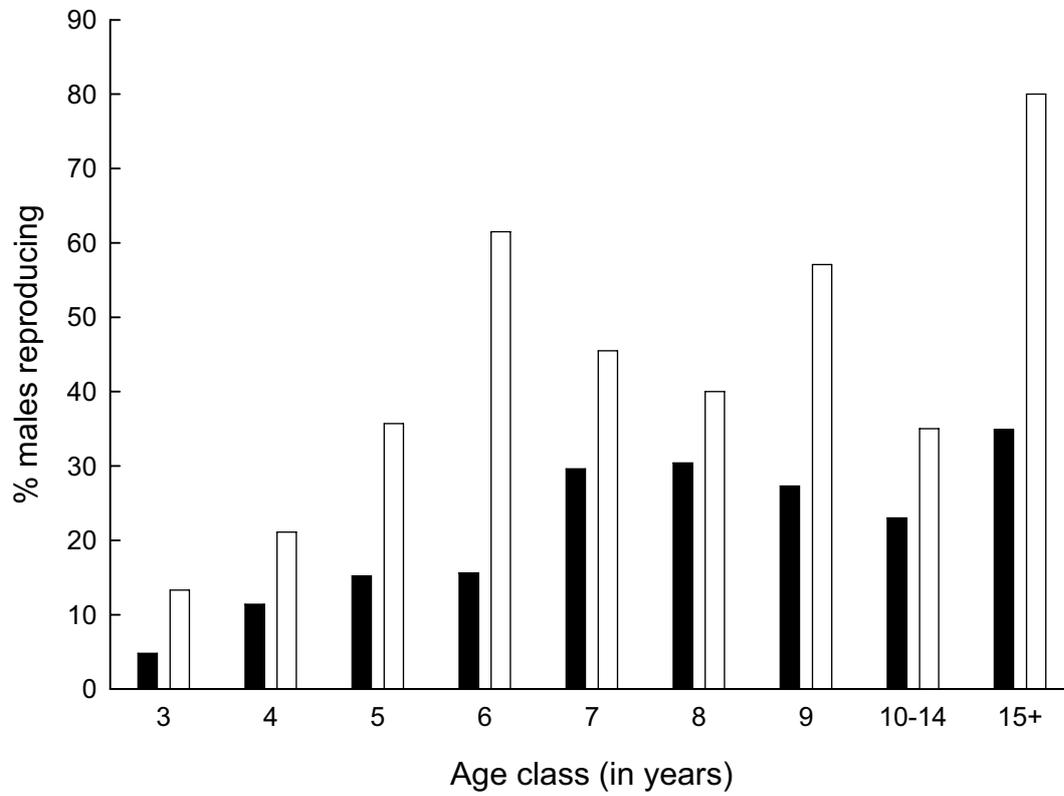
51

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
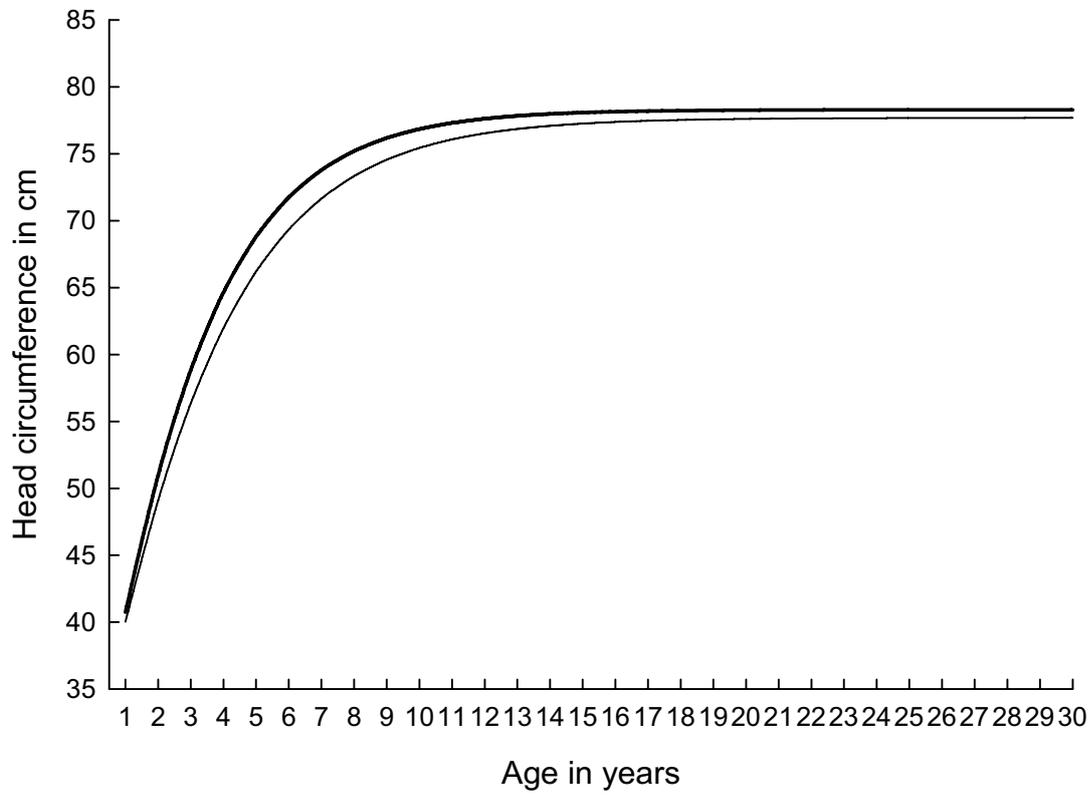
Paper IV

"Do we use our heart, our genitals, or our brains in mate selection?" –
Anonymous

The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide

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Because of differential investment in gametes between sexes, females tend to be the more selective sex. Based on this concept, we investigate mate selection in a large carnivore: the brown bear (*Ursus arctos*). We hypothesize that, in this species with sexually selected infanticide (SSI), 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 largest, most heterozygous and less inbred and also the geographically closest males were more often the fathers of the female's next litter. We suggest 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.

Keywords: female choice; infanticide; mating system; microsatellites; parentage analysis; *Ursus arctos*

1. INTRODUCTION

Mate selection is defined as the process leading to the tendency of members of one sex to mate non-randomly with respect to one or more varying traits in members of the other sex (Heisler *et al*. 1987). It is a component of the intersexual conflict and an evolutionary force driving mating systems (Darwin 1871; Andersson 1994). 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 & Møller 1993; Eberhardt 1996). Why and how females select their partners and how mating preferences have evolved remains under debate among evolutionary biologists and understanding these mechanisms is one of the greatest tasks in behavioural ecology (for a review see Cordero & Eberhard 2003).

Several surrogate measures of male quality have been used to evaluate female choice. Morphological traits, such as body size, weaponry and intense signals of fighting ability, are essential in male–male competition and are expected to be important cues in female choice (Andersson 1994), as is male age (viability selection theory; Trivers 1972), provided that survival rates are not age-dependent (Beck & Powell 2000). Females may also gain genetic benefits by selecting the most heterozygous males (the 'good genes' hypothesis; Brown 1997). Assuming a correlation between heterozygosity and fitness-associated traits (Hansson & Westerberg 2002), 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. Also, by choosing mates based on compatible genes such as the Major Histocompatibility Complex (MHC), females may enhance their offspring viability and performance (Penn & Potts 1999; Trezenga & Wedell 2000). Finally, mate selection directed towards less related individuals has been suggested as an efficient mechanism for inbreeding avoidance (Blouin & Blouin 1998). Generally, these surrogate measures of male quality are tested separately. Limited by the availability of field or genetic data, and also by appropriate statistical models, very few studies have included several of these factors in the same model to determine the extent each factor influences female mate selection.

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

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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 prioritize 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 hypothesized as a major factor explaining multi-male mating by female mammals (Wolff & Macdonald 2004). Based on this hypothesis, females would tend to mate with any males they are likely to meet in the future, while accompanied by their dependent young, rather than trying to select a high-quality partner. Wolff & Macdonald (2004) pointed out that future studies should quantify the role of female choice to elucidate the evolutionary significance of multi-male mating in female mammals.

The mating system of bears, including mate selection, is poorly known. To our knowledge, only a few studies have examined this question in brown bears (*Ursus arctos*; Craighead *et al.* 1995*a*, 1998) and American black bears (*Ursus americanus*; Schenk & Kovacs 1995; Kovach & Powell 2003), all with a limited number of genetic samples and field observations. Female bears are induced ovulators, i.e. eggs are released after behavioural, hormonal or physical stimulation (Craighead *et al.* 1995*b*; Boone *et al.* 1998). This may allow females to evaluate male quality inside the reproductive tract and may provide them with more control over the paternity of their offspring than with spontaneous ovulation (Larivière & Fergusson 2003).

Based on the assumption that female bears may be choosy, we investigated female mate selection in two subpopulations of Scandinavian brown bears that have been studied for about 20 years and for which good field and genetic data are available. SSI has been documented in these subpopulations (Swenson *et al.* 1997; Swenson 2003), and it has been shown that infanticidal males were not related to the cubs they killed (Bellemain *et al.* 2005*a*). Males seem to be able to differentiate their own cubs from unrelated cubs, perhaps by recognizing the females they mated with the year before.

Based on paternity assignment of the female's litter, we tested the following predictions:

(1) females select males based on morphological, age or genetic criteria to maximize their reproductive output or inclusive fitness (direct or indirect benefits). Based on theory and the literature review described above, we predicted that paternity assignment would be positively correlated with male age, body size, and negatively correlated with a male's internal relatedness (an index reflecting both heterozygosity and inbreeding; see §2) and his relatedness to the female; and

(2) females use a strategy to minimize the risk of SSI by confounding paternity, i.e. mating with the geographically closest males, which have the highest potential to kill their future cubs.

2. MATERIAL AND METHODS

(a) *Study species, study areas and sampling*

During the mating season, male and female brown bears remain together for a few hours to several days, or even several

Table 1. Number and percentage of brown bears for whom the mother and/or father have been determined genetically or verified (from prior field observations) with a parentage probability greater than 80%, in two study areas in Scandinavia.

	determined paternities	maternities	
		genetically determined	verified from field data
north study area (*n* = 148)	96 (64.8%)	12 (8.1%)	113 (76.3%)
south study area (*n* = 248)	146 (58.9%)	31 (12.5%)	160 (64.5%)
total (*n* = 396)	242 (61%)	41 (10.4%)	273 (68.9%)

weeks (Craighead *et al.* 1995*b*), and both males and females mate promiscuously, with females mating with up to eight males in a mating season (Craighead *et al.* 1995*b*). Both sexes roam to mate, increasing their home range during the early May to mid-July mating season (Dahle & Swenson 2003*a*). Implantation is delayed until November (Renfree & Calaby 1981). After 6–8 weeks of effective gestation, females give birth to 1–4 small cubs in January, while still hibernating in dens (Pasitschniak-Arts 1993). Young bears receive extended maternal care, staying with the mother for 1.5–2.5 years in the studied populations (Dahle & Swenson 2003*b*). Females do not mate while caring for their young (Schwartz *et al.* 2003) and there is no paternal investment in rearing of the offspring. A previous study (Bellemain *et al.* 2005*a*) showed that multiple paternities were frequent in this population, occurring in 14.5% of 69 litters with greater than or equal to two young and 28% of 32 litters with greater than or equal to three young. Scandinavian brown bears exhibit a sex ratio close to 50 : 50 (Bellemain *et al.* 2005*b*). Cub mortality averages 35% annually in the southern study area and 4% in the northern study area (Swenson *et al.* 2001). A study examining nutritional, social, (SSI), and den disturbance factors found that the patterns of cub mortality were best explained by social factors in both populations (Swenson *et al.* 2001).

The study areas are located in southcentral Sweden (49 000 km²) and northern Sweden (8000 km²) and are described by Bjärvall & Sandegren (1987). The two subpopulations located in each study area differed in mortality regimes and in their male age structure. Bear hunting was, generally, allowed during the autumn in both areas, but the northern area included three national parks, where bear hunting was illegal during the study period, although there was evidence of intensive poaching (Swenson & Sandegren 1999). There were few large adult males in the northern study area and a more evenly distributed male age structure in the southern study area (Swenson *et al.* 2001).

We used radio-telemetry for long-term monitoring of adult bears. Between 1984 and 2003, brown bears, including females accompanied by their yearling offspring, were immobilized in the spring and received radio-transmitters. Home ranges of radio-marked bears were estimated using 95% Minimum Convex Polygon as described by Dahle & Swenson (2003*a*). In addition, we obtained teeth for age determination and location of death from all killed bears (legally hunted or traffic-killed) in Sweden. Tissue samples
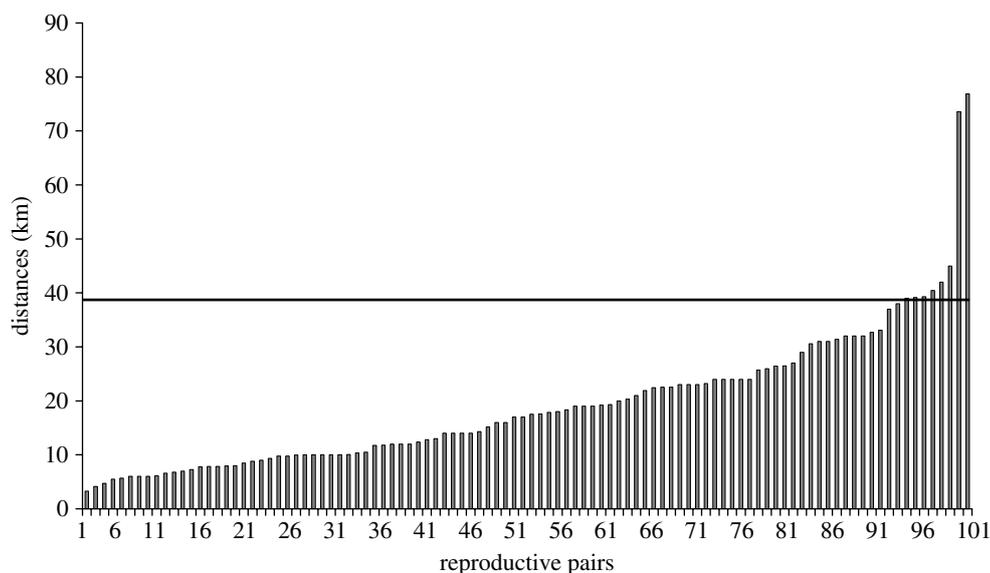
Figure 1. Geographical distances between the centres of the home ranges (or kill location) of 102 reproductive pairs (determined from parentage analysis) of brown bears in two populations in Scandinavia. The horizontal black line represents the distance corresponding to the 95% of the distribution of the distance between reproductive pairs (40 km).

were collected from both marked and killed bears and stored in 95% alcohol until extraction for genetic typing.

(b) *DNA extraction and typing*
Our genetic database contained 977 bear genotypes, of which 396 were from marked animals. The amplification and analysis of microsatellites were carried out following the protocol described by Waits *et al.* (2000). The following 18 microsatellite loci were used: G1A, G1D, G10B, G10C, G10L, G10P, G10X, G10H, G10O, G10J (Paetkau & Strobeck 1994; Paetkau *et al.* 1995) and Mu05, Mu10, Mu15, Mu23, Mu50, Mu51, Mu59, Mu61 (Taberlet *et al.* 1997).

(c) *Parentage analysis*
Based on the multilocus genotypes of mothers, offspring and males, we analysed parentage using the software PARENTE (Cercueil *et al.* 2003, available at http://www2.ujf-grenoble.fr/leca/membres/manel.html). One allelic incompatibility of 18 loci was allowed in the comparison of the parent–offspring genotypes to account for possible genotyping errors or mutations. We assessed the proportion of individuals for which parentage was assigned in the population (table 1). The results were checked with observational field data and for geographical consistency.

(d) *Evaluation of female choice*
We evaluated selection of reproductive partners by radio-marked oestrous females based on the comparison of characteristics of males that became fathers of the subsequent litter and other males in the vicinity of the female that did not become fathers. We proceeded in two steps:

(1) we considered geographical information (radio-telemetry data for marked bears or kill location for unmarked bears) of all males in the vicinity of each radio-marked oestrous female as potential reproductive partners (hereafter referred to as 'large dataset'); and
(2) to evaluate further if females actually had the opportunity to choose among males, we considered only observed (visually or radio-telemetry) cases of female–male

encounters during the mating season (hereafter referred to as 'behavioural dataset').

The data selection and evaluation of female mate selection is detailed below for each of the datasets.

(i) *Data selection for the large dataset*
A male was considered available for potential reproduction with a given female if three criteria were fulfilled: (i) he was at least 3 years old (age of sexual maturity in male Scandinavian brown bears; our unpublished data) during the year the female was in oestrus; (ii) he was known to be alive during the female oestrous year (based on radio-tracking or killed-bear data); (iii) his home range centre (or kill location for unmarked males) was located within 40 km of the home range centre of the oestrous female. This 40 km distance corresponds to the 95% distribution of the distances between all reproductive pairs, known from parentage analysis (i.e. distance between the centres of the respective home ranges or kill locations; figure 1). This distance was chosen rather than the maximum distance between reproductive pairs to avoid overestimation of the number of males available in the vicinity of the female. Also, this distance seems reasonable based on behavioural data from both males and oestrous females during the mating season; oestrous females travelled a mean of 5.25 ± 0.47 km per day (range 0–24.9 km) and males travelled a mean of 13.25 ± 1.05 km per day (range 0.1–42.4 km) in our southern study area (Kristoffersen 2002).

Female choice was evaluated in relation to the following explanatory variables: (i) *study area*, as a factor variable; (ii) *number of males available around the oestrous female*, i.e. the number of males at a distance less than or equal to 40 km from the centre of the female's home range; (iii) *Male age*, as determined from field data. For all bears that were not captured as yearlings of radio-marked females, we collected a first premolar for age estimation based on the cementum annuli in the tooth root (Matson *et al.* 1999); (iv) *Male internal relatedness* (IR). This IR index reflects a quantity measured between parental half-genotypes. It is an estimator of heterozygosity, giving more weight to homozygotes

Table 2. Summary of a generalized mixed linear model analysis of female brown bear choice in Scandinavia as a function of: number of males available (within a radius of 40 km around the female), study area, geographical distance between the home range centres of the male and female, male body size, male IR and relatedness between the male and female. (The response variable was assumed to be binomial, given random effect for female identity. After a successive exclusion of the least significant terms ($p \geq 0.05$), the significance values of the final model are shown in the table. Non-significant terms are presented with the values they were removed from the model with. d.f. is degrees of freedom, β is the logistic regression coefficient, s.d. is the standard deviation, s.e. is the standard error, t denotes the t-value and p the significance level. Number of observations, 837 and number of groups, 48.)

explanatory variables	β	s.d.	s.e.	t	d.f.	P
fixed effects						
area	−0.0238		0.3226	0.0738	46	0.9415
relatedness	0.3182		0.5619	0.5662	773	0.5714
number of males available	−0.1375		0.0251	−5.4823	773	<0.0001
male IR	−2.426		0.7189	−3.374	773	0.0008
male body size	0.0485		0.0163	2.9699	773	0.0031
geographical distance	−0.0373		0.0112	−3.3157	773	0.0010
intercept	−2.7080		1.2509	−2.1648	773	0.0307
random effects						
female identity		0.0114				
residual		1.0219				

involving rare alleles. It is calculated as:

$$IR = \frac{2H - \sum fi}{2N - \sum fi}$$

(Amos *et al.* 2001), where H represents the number of homozygous loci within an individual, N the number of loci genotyped and fi the frequency of the ith allele contained in the genotype; (v) *Male body size*, using head circumference (at the widest part of the skull using a tape measure) as a surrogate measurement of absolute size of an individual. To estimate absolute size in the years a male was not captured, we calculated the von Bertalanffy growth curve (von Bertalanffy 1938) for each subpopulation. 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 (our unpublished data); (vi) *Genetic relatedness between a female and her potential reproductive partners*, pairwise relationship coefficients ('r' as defined by Wang 2002 and recommended in Blouin 2003) were calculated for any two individuals by comparing the shared alleles of these individuals with the allele frequencies in each subpopulation, using the software SPAGEDI (Hardy & Vekemans 2002, available at http://www.ulb.ac.be/sciences/lagev/spagedi. html); and (vii) *Geographical distance between potential reproductive partners*, calculated as the distance (in km) between the centres of the respective home ranges or kill sites.

Variables i and ii were used as control variables; female choice might differ between study areas, as those areas differed in their male age structure and mortality regimes, and may be influenced by the density of males available in the vicinity. Using variables iii–vi, we tested whether female choice was influenced by male quality (prediction 1) and, using variable vii, whether female choice was influenced by SSI (prediction 2).

(ii) *Data selection for the behavioural dataset (see table 3)*
We selected visual or radio-telemetry observations of oestrous radio-marked females with at least one known male during a mating season and when the father of her next year's litter was genetically determined. Female choice was evaluated in relation to the following explanatory variables (as described

above): male age; male IR; male absolute body size; genetic relatedness between the female and her potential reproductive partners. In this case, comparing the other variables described above (study area, number of males in the area, geographical distance) was meaningless.

(e) *Statistical analysis*
We evaluated female choice based on paternity assignment of the female's next litter, i.e. whether or not a particular male was the father of a female's cubs (binomial process). For the large dataset, we used a generalized linear mixed model (GLMM) with a logit link and binomial error distribution (McCullagh & Nelder 1989) to account for the effects of the explanatory variables on the probability of paternity assignment. The response variable (paternity assignment) was assumed to be binary ('1' for a male(s) genetically determined as a father(s) or '0' for all other males within a 40 km radius), given random effects for female identity. Models were fitted using a penalized quasi likelihood method (Venables & Ripley 1999) in the statistical software R 1.9.1 (R Development Core Team 2004, http://www.R-project.org). After a stepwise exclusion of the least significant term ($p \geq 0.05$), the final model was revealed. Models were compared using the AIC criterion (Burnham & Anderson 1998).

For the behavioural dataset, we used pairwise t-tests to compare characteristics of males that were observed with oestrous females during the mating season with characteristics of the actual father(s) of the females' next litter. The software SPSS (SPSS 12.0.1, SPSS Inc., Chicago, IL) was used for those statistical analyses.

3. RESULTS
(a) *Parentage analysis*
All mother–offspring combinations known from field observations ($n = 314$) were genetically confirmed (table 1). In addition, we genetically determined the maternity for 41 marked bears with unknown pedigree (table 1). Paternity was genetically determined for 242 (61%) of the marked individuals; 6% of those fathers were unmarked.

Table 3. Observations (visual or radio-telemetry) of radio-marked female brown bears for which the paternity of the next year's litter was determined.

case[a]	female[b]	year	father(s)[b,c]	males observed together with the female[b,d]
1	BD01	1991	BD06	BD06 on May 16, 17; BD34 on June 2, 4
2	BD01	1997	BD59; 01BD02	BD59 on May 29; both BD50 and BD38 on June 11
3*	BD01	2000	unmarked	BD105 on June 8
4	BD07	1993	BD06; BD43	BD43 on May 26, 27 and June 15
5	BD07	1995	BD35	BD35 on May 16, 24, 28 and June 2; BD06 on June 8, 13
6*	BD10	1988	unmarked	BD17 on May 25, 30 and June 1, 3
7*	BD104	2000	BD06; BD38	Both BD36 and BD73 on May 18; BD73 on May 22
8*	BD12	1990	BD60	BD32 on May 31 and June 3
9*	BD18	1988	unmarked	BD09 on June 6, 7
10*	BD23	1994	unmarked	BD35 on May 12, 16, 19, 25
11	BD23	2001	BD36	BD36 on June 1; both BD36 and BD97 on June 4
12*	BD24	1992	BD34	BD40 on May 15, 18, 21; BD34 on May 20, 23, 25; BD06 on June 1
13	BD27	1990	BD06	BD06 on May 17, 18, 21, 22, 23, 25; BD34 on June 5, 8
14	BD37	1995	BD36; BD61	BD36 on June 2; BD38 on June 8
15*	BD47	1996	BD06	BD38 on May 28, 29 and June 3
16	BD71	2000	BD88	BD88 on May 18, 22, 31; BD36 on June 8
17*	W8802	1988	03ZZ17; unmarked	W8801 on May 21
18*	W8808	1990	W8503	W8903 on July 4, 7
19*	W8808	1994	W9011; unmarked	both W9301 and W8607 on May 20; W9301 on May 29; W9301 on June 16, 17
20*	W8904	1995	99X02	W9202 on June 24
21*	W8906	1989	W8607	W8903 on May 21; W8503 on May 28
22*	W8906	1993	W8607	W9301 on May 18, 21; W8607 on May 24; W8607, W9301 and 2 unmarked males on May 28, 29; W8607 on May 30; W9301 on June 4, 5, 8
23*	W8906	1995	unmarked	both W8607 and W9511 on June 21; W8607 on June 23
24*	W8906	2001	W0012	W9301 on May 21
25*	W9003	1997	W0108; unmarked	both W8807 and 1 unmarked male on May 21
26	W9008	1998	W9505	W9505 on May 19 and June 12, 13; both W9311 and W9505 on May 24
27*	W9403	2000	W0232; unmarked	W0016 on May 31
28*	W9615	2001	W0233	W9921 on June 6, 9

[a] Asterisks indicate situations where the father, or one of the fathers, was not the first male observed with the mother during the mating season.
[b] Identification numbers: BD, from the northern study area; W, from the southern study area; numerical, unmarked bears killed during the hunting season (their data was subsequently recorded).
[c] Male(s) genetically identified as the father(s) of the female's next litter (cases 1, 4, 7, 14, 17, 19, 25, 27 represent cases of multiple paternity).
[d] If the female was observed with an unmarked bear and this individual showed obvious mating behaviour (copulation, tending, fighting with marked males), then this bear is referred to as observed.

(b) *Female choice*

The large dataset included 43 litters in the southern subpopulation (24 mothers) and 52 litters in the northern subpopulation (24 mothers). Totally, 107 different males were considered available (of which 20 were unmarked) for a total of 825 bear-years, and 102 reproductive pairs were considered (including 7 litters with multiple paternity with both fathers known). Two litters (*ca* 2%) resulted from incestuous matings (reproduction between the daughter and her father). The distance between reproductive pairs ranged from 3.3 to 76.8 km (figure 1). A minimum mean of 12.48 ± 5.33 (s.e.) males (range 3–25) in the south and 7.82 ± 3.81 (s.e.) males (range 2–16) in the north were known to be available in the vicinity of a given female (within a radius of less than or equal to 40 km) during her oestrous year.

Male age and male body size were highly correlated (Pearson correlation; $r = 0.657$; $P \leq 0.001$). We therefore analysed these variables in separate models, including all other explanatory variables. The model including male body size was kept instead of the one including age, as it had a lower AIC value. The results of the final GLMM (table 2) showed that paternity assignment was positively correlated with male body size and negatively correlated with male IR, with geographical distance and with the number of males available within a 40 km radius.

The explanatory variables 'study area' and 'genetic relatedness' did not significantly influence paternity assignment. All possible interactions making biological sense were tested in the model, but none of them were significant. The random effect of female identity was small (s.d. = 0.0114) in our study, and it only slightly modified the estimates of the final model. All other models (results not shown) had a difference in the AIC value greater than 2 and were thus not considered in the discussion.

The behavioural dataset (table 3) included 12 litters in the southern subpopulation (eight mothers) and 16 litters in the northern subpopulation (12 mothers). There was considerable variation in the observations of female–male encounters. In eight of 28 cases (28.5%), females were observed with two or more males at the same time; in all other cases, they encountered males sequentially. Thirteen females were observed with only one male, 13 females with two, one female with three males and one female with five different males during the mating season. Overall, 54% of the females were observed with more than one male during the course of a mating season. In 12 cases (43%), the female was observed with the father of her next years' litter. We did not observe any cases of females rejecting a male, nor have other observational studies of brown bear mating behaviour (Craighead *et al.* 1995b), however this is extremely difficult to document. We observed several

instances of apparent long-term association (greater than 4 days) between a male and a female, without the male becoming a father (table 3). Most of the time (in 68% of the cases), the first male to be observed with the female was not the father of the subsequent litter. Females observed in more than one mating season did not always reproduce with the same male (e.g. BD07 reproduced with BD06 and BD43 in 1993 and with BD35 in 1995).

Pairwise *t*-tests showed that paternal males were significantly older ($t_{20} = 3.36$; $p = 0.003$) and larger ($t_{14} = 3.28$; $p = 0.005$) than males that did not become fathers. We did not find a difference in IR ($t_{27} = -0.25$; $p = 0.808$) nor relatedness to the female ($t_{27} = -0.58$; $p = 0.568$) between the fathers and other males.

4. DISCUSSION

(a) *Distinguishing between female choice and male–male competition in paternity assignment*

Sexual selection predicts that the fundamental reproductive asymmetries between males and females give rise to a conflict between sexes (Darwin 1871). In mammals, females are typically choosy, as they invest the most into reproduction (Darwin 1871; Clutton-Brock 1989). Even if females do not choose their mate before mating, they may still have the post-mating opportunity to choose between the sperm of several males (cryptic female choice; Eberhardt 1996). However, male–male competition can also occur during the post-copulatory phase via sperm competition (Ginsberg & Huck 1989). It is extremely difficult to distinguish between those two aspects of sexual selection and to evaluate their relative importance. For instance, 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 out-compete other sperm; Gomendio & Roldan 1993) under controlled conditions (e.g. Hugues *et al.* 1999).

In this paper, we chose to focus on the evaluation of 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. During the pre-copulatory phase, both sexes seem to play a role in paternity determination. Brown bears show large size dimorphism, with males being 1.2–2.2 times heavier than females (Stringham 1990), revealing the importance of intra-sexual selection, through male–male competition, for gaining access to females (Andersson 1994). Meanwhile, females roam extensively during the mating season (Dahle & Swenson 2003*a*), suggesting that they are actively searching for copulations, perhaps to confound paternities in the context of SSI. We did not observe females rejecting any males, which otherwise would argue against the SSI hypothesis. We documented that some highly reproductive males (our unpublished data), which, under a sperm competition hypothesis would have highly competitive sperm, were not always fathering the cubs after being observed with a female (e.g. table 3, cases 5 and 12 for male BD06). Thus, the sperm of dominant males does not always result in paternity, perhaps due to sperm selection by the female.

Females encountered males simultaneously as well as sequentially. In the first case, females may be able to assess male quality by direct comparison. In the second case, selection inside the female reproductive tract via sperm selection or sexual stimulation may allow a female to gather information to compare several males simultaneously. We suggest that, by being promiscuous, females might mate with the geographically closest partners (as a counter-strategy to infanticide), and select a father for their offspring via post-copulatory choice. In the following section (§4b), we concentrate on mechanisms influencing female mate selection, although sperm competition cannot be ruled out.

(b) *Factors influencing female choice*

Optimal choosiness should be affected by at least three variables: distribution of mate quality, cost of searching for mates, and the chooser's quality (Gibson & Langen 1996). We were not able to evaluate the costs of searching for mates. However, the other two variables (distribution of mate quality and chooser's quality) were considered in our model. In our study, some observations were made of the same individual in different years and are consequently correlated, because both are modelled as a function of the same random effect, female identity. The GLMM considers the effects of 'female identity' (the chooser here) as a random factor (predicted as individual-specific deviations from a population mean once the independent effects of other variables are accounted for) and removes the effect of statistical dependence among repeated measures. As predicted, the number of males available around a given female had a significant effect on female choice. Therefore, by including this variable in the model, the effects of the other explanatory variables were corrected for.

Paternity assignment was negatively correlated with male's IR in the large dataset. This index reflects parental similarity better than commonly used heterozygosity indices (Amos *et al.* 2001). For example, negative values are suggestive of relatively outbred individuals, whereas high positive values suggest inbreeding. This negative correlation suggests that females would select both highly heterozygous and less inbred males, which will in turn favour the production of diverse and superior offspring (Brown 1997). Heterozygosity is probably linked to male quality via the functional overdominance hypothesis (Hansson & Westerberg 2002) and females might select their partners based on condition-sensitive traits in the male, such as body size, symmetry or other external features. This paternity bias toward more heterozygous and less inbred males may be explained by post-copulatory mechanisms inside the female reproductive tract. Either the most heterozygous sperm outcompete the rest by being the fittest (Ginsberg & Huck 1989), or a female is able to evaluate male sperm quality and select the most heterozygous sperm (Birkhead & Møller 1993). Nuclear heterozygosity might also be linked to polymorphism in MHC, with females obtaining indirect benefits from choosing males with the most compatible MHC genes (Penn & Potts 1999; Trezenga & Wedell 2000). MHC-based disassortative mating preferences would reduce homozygosity throughout the genome, and particularly within loci linked to the MHC. Progeny derived from such matings would have an increased
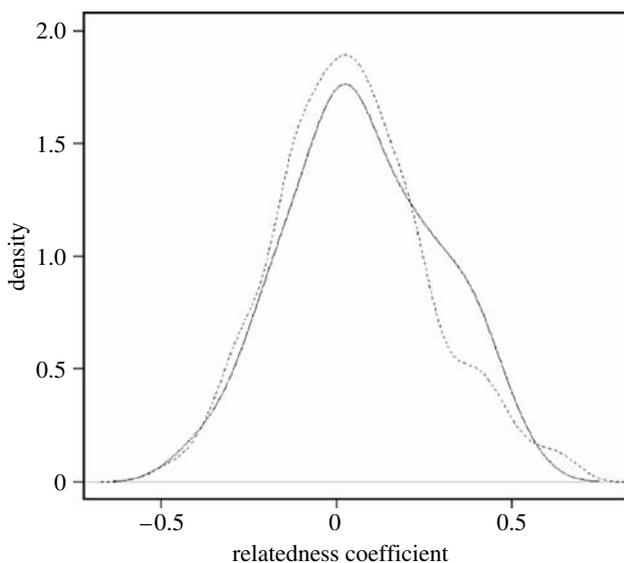
Figure 2. Distribution of relatedness coefficients between reproductive pairs (solid line) or potential pairs (dotted line) of brown bears in Scandinavia within a 40 km radius.

fitness, because of reduced levels of inbreeding and increased resistance to infectious diseases arising from their increased MHC heterozygosity. This hypothesis has, to our knowledge, only been tested with laboratory animals (e.g. Yamazaki *et al.* 1978) and remains to be investigated in wild mammals. The finding of interactions between parental male and female genotypes calls for studying the physiological mechanisms involved (Bernasconi *et al.* 2004). The lack of significance of the IR factor in our behavioural dataset could be due to low power caused by small sample size.

The morphological factor 'body size' was positively correlated with paternity assignment both in the final model of the large dataset analysis and in the 'behavioural data' analysis. As previously suggested, large body size in males could reflect their genetic quality and females may select their reproductive partner based on this criteria. Body size is age-dependent in bears (male age and male body size were highly correlated in our data; see results), therefore females choosing the largest males also select for the oldest males, although the age variable was less important than body size in paternity assignment. In several mammals, age is correlated with dominance rank and it has been shown that dominant males obtain higher reproductive success (e.g. in red deer (*Cervus elaphus*); Clutton-Brock 1988). We have no data on dominance status of males in our subpopulations, however male bears do not defend exclusive territories but have overlapping home ranges (McLellan & Hovey 2001). Thus they may interact with each other throughout the year and a male dominance hierarchy may be established, as suggested in American black bears (Kovach & Powell 2003). Therefore, selection of older males by females might also reflect selection of dominant males.

Among all males available within a 40 km radius, paternity assignment was negatively correlated with geographical distance to potential reproductive partners. In these subpopulations, where SSI is prevalent and where infanticidal males are mostly residents (Swenson *et al.* 1997, 2001; Swenson 2003), it has been proposed that females use promiscuity as a counterstrategy to SSI

(Swenson 2003; Bellemain *et al.* 2005*a*). In this study, we further suggested that female mating behaviour is influenced by the occurrence of SSI as the geographically closest males, i.e. potentially infanticidal males, were preferentially selected as fathers of the offspring. We suggest that females may chose to mate with as many close males as possible, which could be viewed as females making 'the best of a bad job' (Wolff & Macdonald 2004). In brown bears, both sexes roam to mate over large distances (Dahle & Swenson 2003*a*), thus individuals whose home range centres 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. females would come into contact with close-living 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. Paternity assignment was not influenced by the factor study area, suggesting that females tended to use the same selection criterion in both subpopulations, independently of the male age structure or mortality regime of the area.

Paternity assignment was not influenced by relatedness between a female and her potential mates in both datasets, indicating that female bears neither prefer genetically distant nor close males. Following the 'optimal outbreeding' theory (Bateson 1983), females should preferentially select males with intermediate relatedness. Relatedness of fathers was not significantly different from non-fathers, either in the large dataset (Mann–Whitney U test; $p = 0.21$; figure 2), nor in the behavioural dataset. This indicates a random mating scheme in relation to relatedness and suggests that mate choice is not a mechanism to avoid overall inbreeding or outbreeding. The spatial organization of bears may explain this pattern. Bears usually exhibit sex-biased natal dispersal: females are highly philopatric and establish their breeding home ranges in or near their natal areas, whereas males disperse from their mothers' home range and can move long distances (McLellan & Hovey 2001). In Scandinavia, about 36% of the females and 85% of the males have dispersed by 4 years of age (O. G. Støen, personal communication). Consequently, the probability of females mating with closely related males is low (except their father, which happened in *ca* 2% of the litters in our dataset) and they do not have to actively avoid inbreeding.

5. CONCLUSIONS

The high number of marked individuals and the large proportion of parentage assignments (table 1) allowed us to study behavioural characteristics in this brown bear population, and to improve our knowledge about female choice in this species. Due to the occurrence of SSI, the optimal strategy for female bears may be to mate with potentially future infanticidal males and exercise a postcopulatory cryptic choice of the father on her offspring. Our findings support this hypothesis, because not only geographical distance, but also male morphological, genetic, and age criteria were important in determining paternity. Females may be able to increase the survival of their offspring by choosing good genes in their reproductive partners (Brown 1997); we suggest that they use

morphological traits such as age or body size and perhaps also dominance status as indicators for male genetic quality. Although our results might partly be explained by male intra-sexual competition, they are consistent with the female choice hypothesis in relation to SSI.

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Paper V

Offspring Abandonment and Maternal Defense as Reproductive Strategies in Brown Bears

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Running head: Abandonment and maternal defense in bears

Elements of the Manuscript for the online edition: appendix A, appendix B

Abstract

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.

Introduction

Species with parental care desert their offspring under certain conditions (e.g. Fair 1978; Bustnes and Erikstad 1991; Fairbanks and McGuire 1995; Szekely and Cuthill 2000). Unprovoked abandonment (i.e. not by human disturbance) in mammals has often been associated with reduced maternal condition, for example in vervet monkeys (*Cercophithecus aethiops sabaeus*) infants are rejected by mothers at the extremes of the reproductive age-distribution or below a critical body mass (Fairbanks and McGuire 1995). Abandonment is most often viewed as detrimental to the mothers' fitness, because it reduces the number of offspring produced in a lifetime. Nevertheless, for a mother in good condition it may pay to abandon a litter of small size or low quality, to shorten the time to the next, probably larger, litter (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 by killing dependent offspring that are not their own, i.e. sexually selected infanticide (SSI) (Hrdy 1979). 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).

The brown bear (*Ursus arctos*) exhibits a variety of reproductive patterns, females have 1-4 cubs-of-the-year (termed cubs here) at intervals of 2-4 years (Pasitschniak-Arts 1993; McLellan 1994; Schwartz et al. 2003a), males exhibit SSI at least in some populations (Swenson et al. 1997a, 2001), and females employ counterstrategies to SSI such as defense of cubs, avoidance of males, and promiscuity (Swenson 2003, Bellemain et al. 2006a). We studied reproductive strategies and maternal care in brown bears by analyzing the causes of cub loss using long-term data on individuals (Swenson et al. 1997a; Sæther et al. 1998; Dahle and Swenson 2003), comparing the results with a behavioral optimization model for defense or abandonment of offspring by female brown bears.

Tait (1980) used the brown/grizzly bear as an example to demonstrate opportunistic abandonment as a reproductive strategy. This strategy can only be of selective advantage if a mother has the ability and the possibility for rapid breeding after losing its young. Female bears come into estrus only if they are not accompanied by dependent offspring, but can become estrous relatively rapidly after losing dependent offspring during the breeding season

(Rogers 1987; Swenson et al. 1997a) and thus can produce another litter the next year. In Scandinavia 8 out of 10 females that lost all young gave birth the following year, compared with none of 40 that successfully raised cubs (Swenson et al. 1997a). Extending the model proposed by Tait (1980), we reevaluate the fitness gain to a mother brown bear by abandoning a singleton cub prior to or during the mating season.

Maternal defense and cub survival should depend upon several factors, including social and nutritional factors. A major social factor affecting bear cub survival is SSI (Swenson et al. 1997a; 2001). Swenson et al. (1997a; 2001) have suggested that cub loss due to SSI in Scandinavian brown bears is positively correlated with the death of adult males 1.5 years earlier in some parts of Scandinavia. Thus we predict that in areas where SSI is suspected to be a major cause of cub mortality, cub loss is higher after the death of one or more adult males 1.5 years ago (termed male turnover) in the vicinity of a given mother with cubs.

Because offspring defense can be very costly for female brown bears (McLellan 1994), they should invest more defending a large litter. Thus we predict that in areas where SSI is suspected to be a major cause of cub mortality, the probability of losing one or more offspring is negatively related to litter size.

We controlled for maternal condition in our analyses, because offspring survival has been reported to correlate positively with offspring condition and maternal condition (Baker and Fowler 1992; Derocher and Stirling 1996; Festa-Bianchet et al. 1997). We controlled for maternal age in the analysis of offspring survival, because Derocher and Stirling (1994) pointed out differences in the age-specific reproductive performance in polar bears (*Ursus maritimus*). We also allowed for a possible effect of maternal body size on cub defense, because large mothers may be better able to successfully defend cubs against male aggressors. In brown bears the costs of maternal defense are probably independent of litter size and can be considerable, because females can be severely wounded or killed by males while defending their offspring (McLellan 1994). We should only expect mothers to adjust their defense in relation to litter size if offspring defense would be costly for them. Therefore we predict that mothers caring for cubs have a higher probability of being killed by males than females with yearlings and adult females without cubs.

Methods

Species Description

The brown bear has a circumpolar distribution and inhabits habitat types ranging from tundra and boreal forest to temperate deciduous forests (Servheen et al. 1999). Age at first reproduction, litter size, and interbirth intervals vary among populations and are linked to body size and condition, which in turn are linked to nutrition (Stringham 1990; Hilderbrand et al. 1999). Reproductive senescence sets in at around age 20-30 (Schwartz et al. 2003b). Brown bears mate from the middle of May until early July, implantation occurs around late November (Tsubota et al. 1989), and cubs are born during hibernation (January-February). The mother and offspring leave the den in April-May. The age of independence varies from 1.4 to 3.4 years (Pasitschniak-Arts 1993), and females usually mate in the season after the offspring are weaned, resulting in interbirth intervals of 2-4 years. Reports of mean litter size range from 1.7 to 2.5 cubs per litter (McLellan 1994; Schwartz et al. 2003a).

Study areas, study populations and field methods

Data for this study were collected in two areas in Scandinavia. The southern study area (south) was situated in Dalarna and Gävleborg counties in south-central Sweden and Hedmark County in southeastern Norway (61º N, 18º E). The northern study area (north) was situated in Norrbotten County in northern Sweden (67º N, 18º E). For a detailed description of the study areas see Zedrosser et al. (in press).

The study populations differed in some demographic parameters (Sæther et al. 1998) (Table 1). Females in the south have a 2-year reproductive cycle and 23% cub mortality, whereas those in the north exhibit 2-or 3-year cycles but only 4% mortality, at least until the late 1990s (Swenson et al. 1997a; Sæther et al. 1998). In the south, 85% of all cubs were lost during the mating season (Swenson et al. 2001), and Swenson et al. (1997a; 2001) proposed that SSI in the south was the main reason for the difference in cub survival. There was little difference in the mean age at first successful litter (south: 5.2 years; north: 5.4 years) or mean litter size (south: 2.4; north: 2.3) (Swenson et al. 2001).

During 1984-2003, 425 different bears were captured (269 in the south, 156 in the north), of which 336 were radio-collared (205 in the south, 133 in the north). The methods used to capture, mark, determine age and radio-locate bears have been described in Dahle and Swenson (2003a). We estimated the reproductive success of females by counting the cubs of radio-collared females from the air or the ground three times during the year; just after leaving

the natal den (late April/early May), at the end of the mating season (early July), and just prior to entering the den in fall (September).

To investigate possible abandonment while still in the natal den, all natal dens in the south (which had the highest cub mortality) were examined for cub remains. For practical reasons, this was not done in the northern study area, which is largely roadless.

Statistical analysis of cub loss

This paragraph outlines the statistical analysis; specifics follow below. Data on cub loss were analysed by logistic regression (Hosmer & Lemeshow 2000), each litter of cubs representing one case. The binary outcome variable was "loss of one or more cubs", and the primary covariates were spring litter size (range 1-4 cubs), maternal size (skull circumference 53-71 cm) and "male turnover", i.e. the recent death of a nearby male within 40 km. In addition, we screened for additional potentially important covariates: age of the mother (range 4-21 years; known to affect reproductive performance in polar bears (*Ursus maritimus*); Derocher and Stirling 1994), year (treated as a continuous variable, a factor, or a random effect), mother ID (random effect), and a yearly population condition index (because offspring survival has been reported to correlate positively with offspring condition and maternal condition; Baker and Fowler 1992; Derocher and Stirling 1996; Festa-Bianchet et al. 1997). Under the null hypothesis that the mortality rate of each cub was equal and independent, the probability of losing at least one cub should increase with litter size. If abandonment was an important cause of mortality, larger litters should have lower cub loss, regardless of male turnover. If SSI were important, recent male turnover should increase cub loss, more so in smaller litters, which were less profitable for mothers to defend. Furthermore, large maternal size should protect against cub loss, especially after male turnover. Our hypotheses regarding SSI imply that male turnover modifies the effects of litter size and maternal size. We therefore fitted models incorporating these statistical interactions.

The proxy for "male turnover" was calculated as the number of bears killed about 1.5 years ago (allowing time for a new male to discover and claim the territory) within 40 km of the centroid of the female's 95% minimum convex polygon range. This included males killed in the hunting season, by accidents, and radio-collared males suspected to have been killed illegally (using the home-range centroid as for females if the location of the kill was unknown). Since 1981, every hunter killing a bear has had to report the sex and kill location and has to deliver a tooth for age determination, as well as body measurements and tissue samples, to the authorities in Scandinavia. A 40-km radius was chosen because Bellemain et

al. (2006a) have shown that 95% of the fathers of cubs occurred within this distance from the mothers. We defined a male as adult when ≥3 years, because the first age of male reproduction is 3 in both study areas (Zedrosser et al., unpublished). The software package Ranges 6 (Anatrack Ltd., 52 Furzebrook Rd., Wareham, Dorset, UK) was used for home range calculation. Because the number of male deaths had a highly skewed distribution and was unlikely to be linearly cumulative, we used the dichotomous predictor "death of one or more nearby adult males" in the analyses reported here.

Extending the method used by Garshelis (1994) and Swenson et al. (2001), we used body mass of yearlings as the basis to construct a population-level index of the general condition of the study populations for each year. We regressed yearling body mass as a function of maternal size, litter size, sex and population density. In this way we controlled for variables that influence yearling mass independently of environmental conditions (Dahle et al., in press). The condition index was defined as the year- and area-specific average of the standardized residuals from this regression.

We considered including random effects of mother ID or year to account for statistical dependence between repeated litters and/or litters in the same year. However, results from fitting such generalized linear mixed-effects models showed no significant random effects, and we therefore report results using ordinary logistic regression.

We analyzed cub loss for each area separately because the circumstances were very different. In the south, cub loss was frequent (Fig. 1) and showed consistent relationships with predictors throughout the study period (1989-2003). In the north, cub loss was very low from 1990 to 1999 (only 2 out of 72 cubs from 30 litters were lost), not allowing statistical inference about any predictors. In contrast, the years 2000-2003 had high cub loss but little variation in litter size (of 19 litters, 11 lost cubs and 16 had 3 cubs). We therefore limited the statistical analysis to the period 2000-2003, noting that there is not sufficient data to estimate any effect of litter size.

Litters of size 4 were rare but had much higher mortality than the others (Fig 1.), perhaps due to energetic and foraging constraints on the mother. To focus on the effects of maternal defense, we decided to omit litters of size 4 from the statistical analysis, although they are included in plots.

We present alternative models based on a forward selection procedure (best-subsets regression gave identical results). Predictor variables were chosen according to their p-values and the AIC-values of the respective models. The analyses were done in R 2.2.1 under Windows; models with random effects were fitted using the lmer-function (package Matrix,

version 0.995-10); models with fixed effects only were fitted using glm-function. Confidence intervals are given at the 95% level.

Model of abandonment

The dynamic optimization model (Mangel & Clark 1988) maximizes the expected future reproduction (number of offspring weaned) of a female brown bear. A mother bear can decide whether to abandon offspring after leaving the den, and whether to defend her litter if she is attacked by a male intending to kill her offspring and mate with her. The state variable in the model is the number and age of the offspring, and the reproductive status of the female (juvenile (1-3 years), mature (>3 years), or senescent but able to care for existing offspring). The mother's age influences her decisions through its relation to reproductive life expectancy. The event sequence in each year is as follows: when leaving the den, a mother weaning offspring receives a "fitness reward", whereas a mother with dependent young may decide to abandon them. Next, a mother with cubs may encounter an infanticidal male, in which case she must decide whether or not to defend her offspring. She may lose her cubs even if she survives a fight (the attacker's desired outcome), but she may also lose her own life. The next event is a possible change in reproductive status, followed by the mating season (hence, elderly mothers who give up their offspring do not "know" whether they will be able to conceive again). Summer and winter involve aging, possible mortality, and the birth of new young by females who were receptive at the beginning of the mating season. The resulting model equations are solved by backwards optimization as described by Mangel and Clark (1988). Refer to the online edition, appendix A for further details on our dynamic optimization procedure.

Our model extends the original abandonment model by Tait (1980) by 1) implementing dynamic optimization, rather than a time-invariant strategy; 2) incorporating an age-dependent model for maturation and reproductive senescence (Schwartz 2003b), rather than assuming 100% mortality at 25 years of age; 3) explicitly representing the behavioral decision to defend against infanticide; 4) in principle, allowing partial litter-size reduction as well as complete abandonment, although partial reduction was never optimal because we retained Tait's (1980) simplified assumption that litter size did not affect the survival of each cub. The demographic parameters of the model were the age of independence, age-specific survival, the proportion of receptive females bearing offspring next winter, and litter-size distribution at the time of emergence from the den. Infanticide parameters were the risk of being attacked, of losing the cubs if attacked, and of both mother and cubs dying if attacked. In addition, we

took as given the parameters for the maturation and senescence model of Schwartz (2003b). Details about the derivation and implementation can be found in appendix A of the online edition. The basic reproductive number (Cushing 2001) is the expected lifetime production of weaned female offspring for a newly-weaned female. We chose this summary statistic because it summarizes fitness over the entire life cycle, can be compared across different life histories, and has a clear relation to population growth rate (R=1 in a stationary population).

Sensitivity analysis of model of abandonment

We assessed the sensitivity to changes in parameter values of our model results regarding the relative advantage of abandonment (or failure to defend) using the ratio of the basic reproductive numbers (R) for a flexible vs. fixed strategy as the response variable. Sensitivities were calculated at parameter scenarios estimated for the south and north in the present data set. Tait's (1980) original model did not include the whole life cycle and therefore does not yield a basic reproductive number, but our aim with the sensitivity analysis is not a detailed analysis of that model in itself.

We report the change in the R ratio resulting from an increase of one percentage point in each of various probabilities: age-specific survival, litter size distribution, probability of attack, and outcome distribution if attacked (both mother and cubs survive; only the mother survives; both mother and cubs die). For litter-size and outcome distributions, we increased one probability at a time, while decreasing the others equivalently, while retaining the relative magnitudes of the other probabilities. If the original probabilites were p_1, p_2, etc., and p_i was increased by d, the new probabilities were $p'_i = p_i + d$, $p'_j = (1-d/(1-p_i))$ for $j{\neq}i$. Without SSI in the model, the R ratio was between flexible abandonment vs. never abandoning. With SSI in the model, the ratio was between flexible abandonment and optional defense, vs. always defending and never abandoning.

Results

Statistical analysis of cub loss

We followed 157 radio-collared mothers with cubs (49 in the north and 108 in the south), of which 65 (41%) experienced partial or total litter loss (13 or 26% in the north and 52 or 48% in the south) (Fig. 1). No evidence was found of abandoned cubs in natal dens.

We found no significant random effects of year or maternal identity in any of the analyses, and therefore report only results from ordinary logistic regression. Furthermore, we found no

significant interactions between male turnover and litter size or maternal size. Below we report results only for models without interaction, noting that their absence may be due to insufficient sample size for some combinations of predictor values.

Male turnover, litter size and perhaps maternal size were the most important predictors of cub loss (Table 2). Here we present the model with all three predictors included, because coefficient estimates and their confidence intervals remained similar in reduced models (see Table 2 for details). The death of a nearby male increased the odds of cub loss by a factor of 3.6 (1.4-9.6, 95% c.i.). Each cub added to a litter reduced the probability that any one of them was lost by a factor of 0.58 (0.31-1.07). Large mothers had a lower probability of losing cubs; the estimated effect of a 5 cm difference in skull circumference was a factor of 0.57 (0.27-1.13).

In the north, the results for the period 1989-1999 are best summarized in words. Only 2 of 30 litters lost a cub, despite 10 litters being near sites where adult males had recently died (Fig. 1). The litters which lost cubs were of size 3 and 4. For the years 2000-2003, logistic regression gave male turnover as the best predictor, the death of a nearby male increasing the odds of cub loss by a factor of about 12 (1.1-139). The effects of other predictors could not be reliably estimated from the limited sample size; in particular, the lack of variation in litter size precluded estimation of any such effect.

We also evaluated the costs of maternal defense. The only natural mortalities among adult females during 1988-2003 were 1 in the north and 2 in the south that were killed by males while caring for cubs (N = 462 bear years; a bear year reflects an individual bear followed for 12 months). The probability of adult females being killed by males tended to be higher for mothers caring for cubs (3 females killed during 204 bear years), than for other adult females (0 females killed during 258 bear years, Fishers exact test, P=0.088). No mother with a singleton was killed in 35 bear years; one mother with a 2-cub litter killed was killed in 81 bear years and 2 mothers with 3- or 4-cub litters were killed in 88 bear years.

Lifetime gain by abandonment.

A mother following a 3-year reproductive cycle and representing the population average (of litter size distribution and survival in different age classes) in the north would gain a 0.97% increase in fitness if she would opportunistically abandon singleton offspring (Table 3). A mother with a 2-year reproductive cycle and representing the population average in the southern population would gain only a 0.04% increase in her basic reproductive number by opportunistic abandonment of singletons (Table 3).

Sensitivity analysis of model of abandonment

The rather low value of "flexibility advantage" was very robust to changes in almost all parameters (less than 0.1% change in flexibility advantage in response to a 0.01 increase in survival, litter-size or attack probability) (Table appendix B1). The single exception was the probability of death from attack, in which a 0.01 increase caused a 0.25% increase in flexibility advantage in the south, and 0.11% in the north. In other words, the option to flee becomes more important if attacks more often become deadly to the mother. This mortality is not expected to be very high, however, because the behavioral strategy of SSI relies on the mother's survival. Further details on the results of the sensitivity analysis can be found in appendix B of the online edition.

Discussion

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. In the south, male turnover was high and associated with cub loss, and cub loss decreased with increasing litter size. In the north, male turnover was low until the last few years, and cub loss increased with increasing litter size, but was consistently lower than in the south. The advantage of abandoning singletons was negligible (0.04%) in the south and small (0.97%) in the north. In comparison, Tait's (1980) original result was a 2.1% improvement in the expected number of offspring. Hence, we rule out opportunistic abandonment, as suggested by Tait (1980), as a major cause of cub loss. Instead, we found that cub loss decreased with increasing litter size, the opposite of what we would expect without the influence of external factors. Willingness to defend seemed to be more important than opportunistic abandonment causing the loss of singletons, because male turnover was the most deciding factor for cub loss. We did not find relationships between cub loss and environmental conditions and maternal age.

Opportunistic abandonment in bears has rarely been reported. Dean et al. (1992) reported anecdotal observations of grizzly bears that could be interpreted as support of Tait's (1980) hypothesis, but it has not been found in polar bears (Ramsay and Stirling 1986; Taylor et al. 1987; Amstrup and Durner 1995), nor have we found reports from other species. The results

of our model calculations showed that if abandonment of singletons would be used as a reproductive strategy, the fitness gain by opportunistic abandonment was highest for females with a 3-year reproductive cycle (Table 3). The fitness improvement is only marginal for mothers in the south, because of their short litter intervals. Most females in the south have a 2-year reproductive cycle, whereas most in the north have a 3-year cycle and almost all in North America have at least a 3-year cycle. Any model-predicted advantage from abandonment applies only in areas with a 3-year reproductive cycle, as the fitness gain with a 2-year cycle was negligible. Changing the age of cub independence in the model from 2 (south) and 3 years (north) to 3 and 2 years, respectively, reversed the fitness gain by abandonment from 0.04% to 0.60% in the south, and from 0.97% to 0% in the north (data not shown).

Brown bears most likely do not abandon offspring while still in the maternal den. Such abandonment would be difficult to observe in the wild, because, in contrast to American black bears (*Ursus americanus*), it is not advisable to visit a female brown bear in the den for human safety reasons. Thus, we did not know the initial litter size at birth, which may have been larger than the litter size we observed after a female had left the den. Due to the time lag between giving birth and leaving the natal den, it is reasonable to assume that a female might decide whether or not to abandon soon after birth, thus avoiding investing energy into these offspring. However, Mano and Tsubota (2002) investigated reproductive characteristics of female brown bears harvested in dens and concluded that embryo loss and neonatal mortality were uncommon. We could not differentiate between failure of conception and offspring abandonment at an early stage. If opportunistic abandonment occurred when leaving the den or shortly thereafter, as Tait (1980) suggested, our methods were adequate to test the model's results. The lack of cub remains in natal dens (this study) suggests that a mother brown bear does not opportunistically abandon single offspring before she has raised them to an age where they can follow her out of the den. 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. Due to the very low and age-dependent gain in fitness it seems unlikely that opportunistic abandonment as a reproductive strategy is selected for.

The death of adult males may promote the influx of immigrating males and/or possibly realignment of the home ranges of adult males (Swenson 2003; McLellan 2005). This would result in males coming into contact with litters that they did not father. The correlation between male turnover and cub mortality has been reported from the south earlier (Swenson

et al. 1997a; 2001). With more data, we now have found indications of it in the north. High initial mortality of adult males and low male immigration rates, apparently due to illegal killing, kept numbers of adult males low (1-3 males) in the north until 1996. Thus, the death of a nearby male did not result in increased probability for the female to encounter infanticidal males until 1999. Then recruitment of locally produced young males and probably increased immigration from the nearby increasing population increased the number of males by 3-4 times (Swenson et al. 2001; Swenson 2003). SSI became evident after the sex and age structure of the population normalized after a period with few adult males and almost no cub loss, as predicted by McLellan's (2005) model of SSI in bears.

The decreasing probability of cub loss with increasing litter size in the presence of SSI in the south is best explained by litter-size dependent variation in maternal offspring defense. 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., Maestripieri and Alleva 1991; Koskela et al. 2000; Jonsson et al. 2002), and other taxa (e.g. Carlisle 1985; Windt and Curio 1986). Anecdotal field observations support the hypothesis of reduced maternal defense activity for singleton litters in brown bears (Troyer and Hensel 1962).

Maestripieri (1992) reviewed the functional aspects of maternal aggression in mammals, and suggested that female aggressiveness during lactation is aimed at protecting offspring. Offspring defense against an infanticidal male is potentially very dangerous for females. In lions the invading males usually commit infanticide after male coalition replacement, and the lionesses of the pride often directly defend the cubs (Packer and Pusey 1984). Packer and Pusey (1983) reported that in two attempted male takeovers, three of five females were wounded and two other disappeared and were assumed to have died as a result of cub defense. Also in bears mothers are severely injured or killed by conspecifics while defending their offspring (Rogers 1987; Garshelis 1994; McLellan 1994, 2005). As predicted, the only adult females in our study that were killed by conspecifics were mothers caring for dependent offspring.

Larger mothers lost fewer cubs, probably due to better defense against sexually selected infanticide. Male brown bears are 1.2-2.2 times larger than females, with the difference increasing with age (Schwartz et al. 2003a). Thus, old, large and experienced females may be able to better defend their cubs, especially against young, not yet fully grown males (McLellan 2005). Maternal size may be more important in the solitary brown bear than in social species, such as lions and primates, in which several females often protect the young

after male replacement or when a female has produced young fathered by a male outside the group (Packer and Pusey 1983; 1984; Sakamaki et al. 2001; Beehner et al. 2005).

The high cub loss in 4-cub litters does not support the conclusion of increased maternal defense for large litters. In both study areas combined, 6 of 8 4-cub litters (75%) experienced cub loss. An exceptionally large litter should theoretically represent a very high value, thus maternal defense should also be high. However factors other than maternal defense might be operating. It may be that a 4-cub litter is above the optimal litter size for brown bears. Farley and Robbins (1995) reported that brown bear cubs are very costly in both relative and absolute terms, and intraindividual variation in mass increases in litter size in both brown and polar bears (Derocher and Stirling 1998; Dahle et al., in press).

Online appendix A: Details on the dynamic optimization model

Notation

Below, the fitness of the focal female is denoted by $f_{\text{(time of year)}}(t, a, n, r)$, where t is the female's age, a and n are the age and number of any offspring, and r is her fertility status. Fertility status is denoted as J, F, and S for juvenile, fertile, and senescent. Fertility status is often omitted for brevity in the equations below, and is taken to be F unless otherwise stated. Age is incremented just before emerging from the den. Thus, $a = 0$ for cubs of the year (a is irrelevant if $n = 0$.) Times of the year are separated by *events*, i.e. stochastic changes in state (see Table A1 for overview and terminology for the different times of the year). Decisions amount to choosing between different (possibly stochastic) courses of events.

Here we explain the model equations in fairly verbose notation, working forward in time. The actual computer implementation used a more compact matrix notation where possible, mapping the multi-dimensional state variable (t, a, n) onto a one-dimensional state index i, and optimizing backwards in the manner detailed by Mangel & Clark (1988). Source code for the model implementation is available on request (Software: Matlab 6.1, The Math Works, Inc.).

From mating season to emergence from den

Aging. - The female's age increases from t to t+1. The age of any offspring increases from a to a+1.

Conception and birth. - For a fertile female of age t with no current offspring, the probability of a transition from state (t, 0, 0), at the start of the mating season, to (t+1, 0, k), on emergence from the den, is $s_t f_k$, where s_t is the female's survival probability and f_k is the litter-size distribution for k = 0 to 4.

Offspring survival. - Assuming equal and independent survival of offspring, conditional on the survival of the mother, the number k of surviving offspring is binomially distributed with n trials and a success probability of s_a. Thus, the probability of a transition from state (t, a, n) to (t+1, a+1, k) is

$$\Pr\left(t+1, a+1, k, \text{at emergence from den} \mid t, a, n, \text{before mating}\right) = s_t \binom{n}{k} s_a^k \left(1 - s_a\right)^{n-k}$$

for $a = 0$ (cubs of the year) to the year before independence ($a = 0$ in the south, $a = 1$ in the north; see below).

Fitness reward: offspring reared to independence. -The fitness currency of the model is offspring reared to independence. Mothers with newly-independent offspring (yearlings in the south, 2-year-olds in the north) receive a fitness reward on leaving the den, and are ready to mate in the upcoming season. The fitness at the time of the mating season for a mother whose offspring will reach independence after the next winter, the only possible transition (except death) is from (t, a, n at the start of the mating season) to (t+1, 0, 0 at emergence from the den), with probability s_t, and the fitness value of her offspring at the beginning of this period is $ns_t s_{a_{ind}-1}$, where the age of independence is $a_{ind} = 1$ in the south, $a_{ind} = 2$ in the north.

Calculating fitness before mating season. - The abovementioned transition probabilities and fitness rewards are used to calculate fitness at the time just before mating season, based on fitnesses calculated for the time of next emergence from the den. The fitness of being in each state (t, a, n) at the start of the mating season is the weighted expectation of future fitness plus the current fitness value of any offspring:

$$f(\text{state } j \text{ before mating season in year } t) = E(f(\text{state } i \text{ at emergence from den in year } t+1))$$

$$= \sum_{\text{all } i} \Pr(\text{transition from state } j \text{ to } i)[f(\text{state } i \text{ at emergence next year}) + \text{fitness reward for transition from } j \text{ to } i]$$

For a given life-history, the transition probabilities may be summarized in a matrix. For illustration, consider fertile females in the north, where offspring wean shortly after age 2 and the maximum litter size is 4. Below is the transition matrix from just before the mating season to just after emergence:

	from R	C1	C2	C3	C4	Y1	Y2	Y3	Y4
to R	f_0	$(1-s_0)$	$(1-s_0)^2$	$(1-s_0)^3$	$(1-s_0)^4$	1	1	1	1
C1	f_1								
C2	f_2								
C3	f_3								
C4	f_4								
Y1			s_0	$2s_0(1-s_0)$	$3s_0(1-s_0)^2$	$4s_0(1-s_0)^3$			
Y2				s_0^2	$3s_0^2(1-s_0)$	$6s_0^2(1-s_0)^2$			
Y3					s_0^3	$4s_0^3(1-s_0)$			
Y4						s_0^4			

($s_t \times$)

Note that 2-year-olds do not appear in the matrix. That is because they are considered to become independent before the time at which fitness is calculated just after emergence. The fitness reward handles the two-year-olds, weighting them by the survival of mother and offspring. The fitness reward associated with each transitions are as follows:

	R	C1	C2	C3	C4	Y1	Y2	Y3	Y4
R	0	0	0	0	0	$s_t s_1$	$2s_t s_1$	$3s_t s_1$	$4s_t s_1$
C1	0								
C2	0								
C3	0								
C4	0								
Y1		0	0	0	0				
Y2			0	0	0				
Y3				0	0				
Y4					0				

For senescent females, the transition matrix is the same except $f_0 = 1$ and $f_k = 0$ for $k > 0$.

For the south, the table is similar, but yearlings do not appear in the matrix:

$$\Pr(\text{from state } j \text{ to } i) = s_t \times$$

	from R	C1	C2	C3	C4
to R	f_0	1	1	1	1
C1	f_1				
C2	f_2				
C3	f_3				
C4	f_4				

The fitness reward associated with each transition is:

	R	C1	C2	C3	C4
R	0	$s_t s_0$	$2s_t s_0$	$3s_t s_0$	$4s_t s_0$
C1	0				
C2	0				
C3	0				
C4	0				

Right after emergence: Abandonment decision

Mothers with dependent offspring face the decision whether to abandon their current young in favor of earlier remating. (The model allows for partial litter-size reduction, which might make sense if offspring survival depended strongly on litter size, but information on this is not available. Thus, the cost is proportional to litter size, whereas the expected benefits from remating depend only on the age of the female. In practice, the model will allow only singleton cubs to be abandoned.)

Abandonment means going from state (t, a, n after emergence) to (t, 0, 0 after abandonment decision). (Partial litter-size reduction would mean going to some state (t, a, $k<n$)). Thus, optimizing this decision amounts to choosing the best possible state that can be chosen. A fixed strategy is modeled by limiting this choice either to never abandon, or always abandon singleton cubs. The fitness of state (t, a, n after emergence) equals the fitness of the chosen "state after abandonment decision". In symbols:

$$f\left(t,a,n \text{ before abandonment decision}\right) = \max_{k \leq n} f\left(t,a,k \text{ after abandonment decision}\right)$$

where a is of course irrelevant if $k = 0$.

Possible infanticide attempt

A female that has cubs in spring is attacked by a male with probability p_A. If the female is attacked, she must choose whether to defend her cubs or not. If she defends, the possible outcomes are: both the female and the cubs survive (probability p_W conditional on the female being attacked and defending the cubs); only the female survives (probability p_L); or both the female and the cubs die (probability $1-p_W-p_L$).

Calculating the fitness of a female before the possible attack is a two-step process, because the behavioral decision to defend is taken only if the female is attacked. For states without cubs, fitness is unchanged through the time at which attacks might occur. For states with cubs,

$$f\left(t,a,n \text{ before attack time}\right) = \left(1 - p_A\right)f\left(t,a,n \text{ after attack time}\right) + p_A f\left(t,a,n \text{ if attacked}\right)$$

where

$$f\left(t,a,n \text{ if attacked}\right) = \max_{\text{run or defend}} \begin{cases} f\left(t,0,0 \text{ after attack time}\right) \text{if the female runs} \\ p_W f\left(t,a,n \text{ after attack time}\right) + p_L f\left(t,0,0\right) \text{if the female defends} \end{cases}$$

The latter choice finds the optimal decision on whether to run or defend.

Change in fertility status

In the model, fertility status may change (from juvenile to fertile or from fertile to senescent) right before the mating season. Schwartz et al. (2003) provide formulas for the probability that a female of given age has matured, and the probability that reproductive senescence has ocurred in at or before a given age. From this we derived age-specific probabilities of

maturation for juvenile females and probabilities of reproductive senescence for mature females (see below). This can be depicted by the following transition matrix:

$$
\begin{bmatrix}
 & J & F & S \\
J & 1 - p_{J \to F}(t) & 0 & 0 \\
F & p_{J \to F}(t) & 1 - p_{F \to S}(t) & 0 \\
S & 0 & p_{F \to S}(t) & 1
\end{bmatrix}
$$

Thus, the fitness of a juvenile female of age t is

$$f(t,0,0,J \text{ before time of fertility change}) = p_{J \to F}(t) f(t,0,0,F \text{ after time of fertility change}) +$$
$$+ (1 - p_{J \to F}(t)) f(t,0,0,J \text{ after time of fertility change})$$

Analogously, the fitness of a fertile female of age t is

$$f(t,a,n,F \text{ before time of fertility change}) = p_{F \to S}(t) f(t,a,n,S \text{ after time of fertility change}) +$$
$$+ (1 - p_{F \to S}(t)) f(t,a,n,F \text{ after time of fertility change})$$

The fitness of a senescent female of age t is unchanged through this time period:

$$f(t,a,n,S \text{ before time of fertility change}) = f(t,a,n,S \text{ after time of fertility change}).$$

End conditions for optimization

Dynamic optimization models are solved backwards in time, and this requires that an end condition is specified. In our case, the end condition is simply $f(t=50, a, n) = 0$. Because only a negligible proportion of model bears will be alive and fertile after this age, the impact of the end condition is negligible. For ages past $t > 0$, any females that are still fertile face an overwhelming probability of senescing before the next mating season. After senescence, females are genetically dead once they wean their current litter, if they have one. Thus, although the model will calculate a sizeable fitness for females aged 50 with cubs, this state is statistically and biologically irrelevant.

Derivation of maturation probability and senescence risk

Schwartz et al. (2003) modeled the probability that a female has had its first litter by age t as

$$\Pr(\text{capable of having a litter at age} \leq t) = p_M(t) = \exp\left(-\left(\frac{t}{\xi_M}\right)^{-\left(\frac{\xi_M}{\theta_M}\right)}\right)$$

where t is the age of the female, $\xi_M = 4.384$ and $\theta_M = 0.626$. This gives the distribution for the age of primiparity, whereas maturation must have occurred before the previous mating season. To derive the transition probability from juvenile to fertile in our model, we make the simplifying assumption that

$$\Pr(\text{first capable of mating successfully at age} \le t) = p'_M(t) = p_M(t+1)$$

This disregards the fact that not all newly-mature females mate successfully ($f_0 > 0$ for fertile females without cubs). Thus, the average age of maturation will be slightly less than that implied by the above equation, slightly down biasing our estimate of the fitness of juvenile females. (This has no effect on the estimated fitness of fertile females, because they are already past the maturation event and fitness is defined as expected *future* offspring production.)

The state-transition probability from J to F in the model is the proportion of females that become fertile shortly after age t, given that they were immature on their tth birthday:

$$\Pr(\text{fertile before breeding season at age } t \mid \text{juvenile at emergence at age } t)$$

$$= \frac{p'_M(t) - p'_M(t-1)}{1 - p'_M(t-1)} = \frac{p_M(t+1) - p_M(t)}{1 - p_M(t)}$$

The denominator is the proportion of females that are not yet mature by age $t-1$, and the numerator is the proportion of all females that mature between ages $t-1$ and t.

The probability that a female is reproductively senescent by age t was modeled as

$$\Pr(\text{senescent at age} \le t) = p_S(t) = 1 - \left(1 - \left(\frac{t}{\xi_P}\right)^{\theta_P}\right) \exp\left(-\left(\frac{t}{\xi_O}\right)^{\left(\frac{\xi_O}{\theta_O}\right)}\right)$$

where t is the age of the female, $\xi_P = 40.269$, $\theta_P = 2.460$, $\xi_O = 28.430$ and $\theta_O = 1.013$. As for maturation, the onset of reproductive senescence will not be observable until next year, when the female fails to produce young, so we assume that

$$\Pr(\text{senescent before breeding season at age } t \mid \text{fertile at emergence at age } t) = p'_S(t) = p_S(t+1)$$

Again, the event in Schwartz et al. (2003) does not correspond exactly to that in our model, because some females that did not have cubs might just have been unlucky rather than incapable of conceiving. Thus, the average age of senescence will be slightly greater than implied by the equation, causing a slight downward bias in the estimated fitness for all

nonsenescent states. However, we believe that this error is negligible compared to other sources of parameter uncertainty. The resulting state-transition probability from *F* to *S* is:

$$\Pr(\text{senescent before breeding season at age } t \mid \text{fertile at emergence at age } t)$$

$$= \frac{p'_S(t) - p'_S(t-1)}{1 - p'_S(t-1)} = \frac{p_S(t+1) - p_S(t)}{1 - p_S(t)}$$

Table A1. The yearly sequence of events in the dynamic optimization model for abandonment of offspring or failure to defend them from attack by mother brown bears. "Events" involve changes in state, usually stochastic. Decisions amount to choosing between different courses of stochastic events, in such a way as to optimize the expected fitness after the next event. The column "Time denotation" is used for reference in the text.

Event	Time denotation	Decision
Leaving den		
	After emergence = before abandonment decision	
		Keep or abandon offspring
	After abandonment decision = before possible attack	
Infanticide attempt		
	If attacked	
		Defend or flee
	After possible attack = before possible fertility change	
Maturation/ Senescence		
	After possible fertility change = before mating	
Mating		
	After mating = before summer	
Birth and over-winter mortality		
	After winter = before emergence	

Online appendix B: Results of sensitivity analysis

Table B1: Results of a sensitivity analysis of a model about the relative advantages of the reproductive strategy of female brown bears "Abandonment (or failure to defend) of offspring" to the changes in the parameter values in two study areas (South, North) in Scandinavia. "Parameters" represents the different parameters as used in the model (Survival age 0-14: age-specific survival; Litter size 0-4: litter size distribution; Probability of being attacked and the outcome distribution if attacked (win: both mother and cubs survive; lose: the mother survives but loses her offspring; die: both mother and offspring die). "Baseline values" represents the parameter values as used to calculate the model; "Change" is the change (in %) in the R ratio resulting from an increase of one percentage point in each of various probabilities of the aforementioned model parameters. For litter-size and outcome distributions, we increased one probability at a time while the other probabilities were scaled down while retaining the relative sizes. With sexually selected infanticide (SSI) in the model, the ratio was between the reproductive strategies "Flexible" (abandonment and defense of offspring is dependent on an optimal choice by the mother bear) and "Fixed" (a mother bear always defends and never abandons her offspring). Without SSI in the model, the R ratio was between the reproductive strategies "Flexible" (abandonment of offspring is dependent on an optimal choice by the mother bear) and "Fixed" (a mother bear never abandons her offspring).

Parameters	Baseline values		Reproductive strategy With SSI Flexible vs. fixed		Change %		Reproductive strategy Without SSI Flexible vs. fixed		Change %	
	South	North	South	North	South	North	South	North	South	North
Survival age 0+	0.77	0.96	1.000000	1.000311	0.00	0.03	1.000000	1.000376	0.00	0.04
Survival age 1+	0.87	0.95	1.000000	1.000000	0.00	0.00	1.000000	1.000000	0.00	0.00
Survival age 2+	0.92	0.94	1.000000	1.000000	0.00	0.00	1.000000	1.000000	0.00	0.00
Survival age 3+	0.95	0.93	1.000000	1.000000	0.00	0.00	1.000000	1.000000	0.00	0.00
Survival age 4+	0.97	0.92	1.000000	1.000000	0.00	0.00	1.000001	1.000000	0.00	0.00
Survival age 5+			1.000003	1.000004	0.00	0.00	1.000010	1.000005	0.00	0.00
Survival age 6+			1.000009	1.000028	0.00	0.00	1.000026	1.000036	0.00	0.00
Survival age 7+			1.000010	1.000080	0.00	0.01	1.000018	1.000094	0.00	0.01
Survival age 8+			1.000011	1.000071	0.00	0.01	1.000020	1.000052	0.00	0.01
Survival age 9+			1.000013	1.000020	0.00	0.00	1.000018	0.999991	0.00	0.00
Survival age 10+			1.000013	1.000037	0.00	0.00	1.000017	1.000061	0.00	0.01
Survival age 11+			1.000014	1.000056	0.00	0.01	1.000017	1.000059	0.00	0.01
Survival age 12+			1.000014	1.000028	0.00	0.00	1.000015	0.999988	0.00	0.00
Survival age 13+			1.000015	1.000024	0.00	0.00	1.000016	1.000032	0.00	0.00
Survival age 14 to ∞			1.000015	1.000035	0.00	0.00	1.000014	1.000049	0.00	0.00

Table B1 continued.

Parameters	Baseline values		Reproductive strategy With SSI				Reproductive strategy Without SSI			
			Flexible vs. fixed		Change %		Flexible vs. fixed		Change %	
	South	North	South	North	South	North	South	North	South	North
Litter size 0	0.200	0.200	0.999924	0.999543	-0.01	-0.05	0.999651	0.999542	-0.03	-0.05
Litter size 1	0.104	0.112	0.999996	1.000491	0.00	0.05	0.999770	1.001600	-0.02	0.16
Litter size 2	0.336	0.360	0.999986	0.999751	0.00	-0.02	0.999948	0.999499	-0.01	-0.05
Litter size 3	0.336	0.256	1.000061	1.000214	0.01	0.02	1.000334	1.000005	0.03	0.00
Litter size 4	0.024	0.072	1.000093	1.000515	0.01	0.05	1.000495	1.000353	0.05	0.04
Probability of being attacked	0.50	0.50	0.999956	0.999721	0.00	-0.03				
Probability to win if defending	0.40	0.40	0.999962	1.000231	0.00	0.02				
Probability to lose if defending	0.59	0.59	0.999952	0.999725	0.00	-0.03				
Probability to die if defending	0.01	0.01	1.002531	1.001069	0.25	0.11				
Age of independence of cubs	1	2								
Maximum age of mother	50	50								
Baseline R flexible			3.642566	2.030695			4.650498	2.463498		
Baseline R fixed			3.640390	2.010606			4.645270	2.410356		
Baseline ratio of R for flexible vs. fixed			1.000598	1.009992			1.001125	1.022048		

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Table 1: Estimated survival parameters (survival of young brown bears from spring to the following spring for a given age) and brown bear litter size distribution used for model calculations in two study areas in Scandinavia.

Survival parameters	age 0	age 1	age 2	age 3	age 4+
Southern study area[1]	0.77	0.87	0.93	0.95	0.97
Northern study area[1]	0.96	0.95	0.94	0.93	0.92
Tait's original data[2]	0.90	0.90	0.85	0.85	0.85
Litter size distribution	0 cubs	1 cub	2 cubs	3 cubs	4 cubs
Northern study area[3]	0.200	0.112	0.360	0.256	0.072
Southern study area[3]	0.200	0.104	0.336	0.336	0.024
Tait's original data[2]	0.150	0.204	0.3655	0.2805[4]	-
Probability of being attacked[5]	0.50				
Probability to win if defending[5]	0.40				
Probability to lose if defending[5]	0.59				
Probability to die if defending[5]	0.01				

[1] Swenson et al. (1997a), Sæther et al. (1998)

[2] Tait (1980)

[3] Sæther et al. (1998)

[4] Tait (1980) combined data for litters of 3 and 4 cubs

[5] These parameters are best judgments based on long-term research on these populations

Table 2. Logistic regression of the probability for a female brown bear to lose at least one cub from spring to fall. Data are from two study areas in Scandinavia (southern study area: 1989-2003, $N = 102$; northern study area: 2000-2003, $N = 19$). Litters of size 4 are excluded from the analysis (for details refer to text). β = estimated coefficient, S.E. = standard error, z = z-value, O.R. = estimated odds ratio (with l.C.I. and u.C.I. denoting lower and upper 95% confidence interval limits), p = p-value, AIC = Akaike Information Criterion. The predictors are "male turnover" = death of one or more males within a radius of 40 km 1.5 years earlier, "spring litter size" = number of cubs of the year in spring , "maternal size" = skull circumference in cm, year, maternal age, "condition index" = population-level condition index.

	Variable	β	S.E.	z	O.R.	l.C.I.	u.C.I.	p	AIC
			Southern study area						
I.	Male turnover	1.11	0.46	2.41	3.03	1.23	7.49	0.016	138.55
	Spring litter size	-0.53	0.30	-1.81	0.59	0.33	1.05	0.071	141.41
	Maternal size	-0.12	0.07	-1.77	0.89	0.77	1.01	0.077	141.48
	Year	-0.05	0.05	-0.91	0.95	0.86	1.06	0.364	143.95
	Maternal age	-0.04	0.05	-0.80	0.96	0.88	1.06	0.422	144.12
	Condition index	0.08	0.24	0.34	1.09	0.68	1.74	0.733	144.66
II.	Male turnover	1.22	Remains as best predictor in I. in the model						
	Spring litter size	-0.63	0.31	-2.01	0.53	0.29	0.98	0.044	136.30
	Maternal size	-0.14	0.07	-1.91	0.87	0.76	1.00	0.056	136.65
III.	Male turnover	1.27	Remains as best predictor in I. in the model						
	Spring litter size	-0.54	Remains as second best predictor in II. in the model						
	Maternal size	-0.11	0.07	-1.58	0.89	0.77	1.03	0.113	135.67
			Northern study area						
IV.	Male turnover	2.51	1.24	2.02	12.25	1.08	138.99	0.043	24.45
	Condition index	-4.06	3.00	-1.35	0.02	0.00	6.13	0.176	27.76
	Year	0.17	0.17	0.97	1.18	0.84	1.66	0.333	28.87
	Maternal size	-0.08	0.13	-0.63	0.92	0.71	1.19	0.532	29.46
	Maternal age	0.08	0.47	0.17	1.08	0.43	2.73	0.863	29.83
	Spring litter size	-17.58	2812.93	-0.01	0.00	0.00	-	0.995	26.18

Table 3. Results of dynamic optimization model for female brown bears facing the decision whether to abandon singleton cubs and whether to defend cubs against infanticidal males. Fitness is defined as the expected future number of female offspring weaned to independence. The model extends that of Tait (1980) by including an age-dependent probability of reproductive senescence, and possibly also a risk of being attacked by infanticidal males. Parameter scenarios correspond to the North and South areas in this study, as well as that of Tait (1980). "Fitness at maturity" refers to the approximate age of primiparity (5 years in Scandinavia, 8 years in Tait's data). The "basic reproductive number" is the expected lifetime production of female offspring (i.e. for a newly-weaned female). The "flexible" strategy allows abandonment of singletons and/or failure to defend against an attacking male. This offers a 0-2% advantage compared to the fixed strategy of never abandoning and always defending. Fitness at maturity for Tait's original fixed strategy of "always abandon a single cub" is included for comparison.

Model features	Parameter scenario	Fitness at maturity				Basic reproductive number		
		Always abandon single cub (Tait 1980)	Flexible	Never abandon, always defend	% advantage	Flexible	Fixed	% advantage
Senescence, SSI	South		8.76	8.86	0.04	3.39	3.39	0.04
	North		4.42	4.37	0.97	1.91	1.89	0.98
	Tait		1.86	1.86	0.15	0.68	0.68	0.14
Senescence, no SSI	South		11.17	11.16	0.09	4.32	4.32	0.10
	North		5.36	5.25	2.18	2.32	2.27	2.19
	Tait		2.28	2.23	2.22	0.83	0.82	1.96
No senescence, no SSI (Tait's 1980 model)	South	18.50	18.52	18.48	0.24			
	North	6.52	6.52	6.38	2.29			
	Tait	2.39	2.40	2.34	2.44			

Figure 1: Loss of brown bear cubs (loss of one or more cubs from spring to fall), litter size in spring, year, and male turnover (whether any adult males were killed 1.5 years previously within 40 km of the home-range center of the mother bear) in two study areas in Scandinavia. Filled symbols indicate cub loss, triangles indicate male turnover. Points are jittered to reduce overlap.
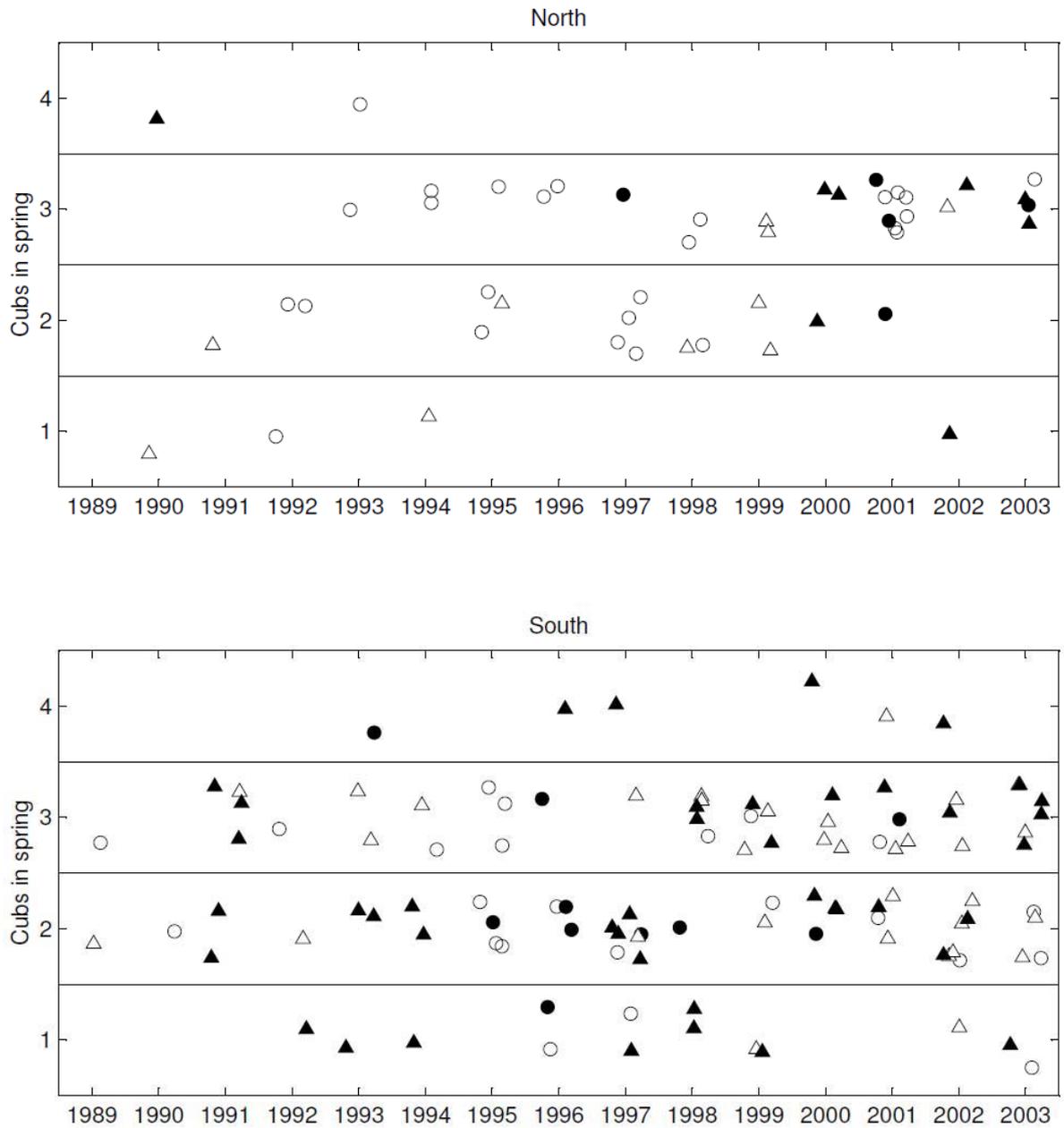
Paper VI

"Maturation divides a life into preparation and fulfillment." –
S. Stearns, "The evolution of life histories"

Primiparity, litter size and cub survival in a species with sexually selected infanticide, the brown bear.

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running title: Primiparity in brown bears

ABSTRACT

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 study 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 southern area 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/experienced in defending their offspring against SSI.

Key words: brown bear, litter size, litter survival, sexually selected infanticide, primiparity, *Ursus arctos*.

Primiparity 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 (Dahle et al., in press). 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 from other bears, which often kill them (McLellan, 1994). For example, males may seek mating opportunities by killing dependent offspring that are not their own, i.e. sexually selected infanticide (SSI) (Hrdy, 1979).

Empirical studies of behavioral strategies and life history of large mammals, especially large carnivores, are rare, because they usually occur at low densities, are long-lived and costly to follow over a long time. Nevertheless, a long-term study of brown bears (*Ursus arctos*) has enabled us to study behavioral strategies in this species. The earliest recorded age of primiparity in brown bears is 3 years (Zedrosser et al., 2004). Litter size is variable in brown bears, ranging from 1 to 4 cubs-of-the-year (termed cubs here) per litter (McLellan, 1994). There is evidence that young and old females produce fewer cubs per litter than prime-age adults (Craighead et al., 1974; 1995; Sellers and Aumiller, 1994). Dahle et al. (in press) found that offspring size was positively related to maternal size and negatively related to litter size and population density. In addition there was a strong cohort effect, suggesting that environmental conditions may be important for yearling brown bear size (Dahle et al., in press).

Brown bears are polygamous, where males compete for access to females in estrous, and females mate with multiple males and may have a litter with offspring sired by different males (Craighead et al., 1995; Schwartz et al., 2003; Bellemain et al. 2006a). Several factors have been proposed as important for brown bear cub survival, including nutritional, social and disturbance factors (McLellan, 2005; Miller et al., 2003; Swenson et al., 1997; 2001),

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however Swenson et al. (1997; 2001) have suggested SSI (a social factor) to be the major agent of brown bear cub mortality in parts of Scandinavia, where 75% of all cub mortalities occurred during the mating season (Swenson et al., 1997). Bellemain et al. (2006b) found all theoretical requirements for SSI to be fulfilled in brown bears.

In this study we evaluated whether primiparous female brown bears show a lower reproductive performance than multiparous females and investigated the probability of cub loss of primiparous females in relation to the SSI hypothesis. Specifically, we predicted that 1) the litter size of primiparous mothers is smaller than of multiparous mothers; 2) the average body size of yearlings with a primiparous mother is smaller than those of yearlings with multiparous mothers; and 3) primiparous mothers have a higher probability of cub loss than multiparous mothers. To analyze the probability of loss of cubs of primiparous mothers we predicted that it is 4a) positively correlated to population density and male turnover (a variable predicting SSI; Swenson et al. 1997; 2001, see methods) and 4b) negatively correlated to environmental conditions, female body size at primiparity, and age at primiparity.

METHODS
Study areas, study populations and field methods
Data for this study were collected in two areas in Scandinavia. The southern study area (south) was situated in Dalarna and Gävleborg counties in south-central Sweden (13,000 km^2, 61º N, 18º E), and the northern study area (north) was situated in Norrbotten County in northern Sweden (8,000 km^2, 67º N, 18º E). The mating season usually lasts from the second half of May until the first week of July in both areas. The snow cover is shorter, mean temperatures in January and July are higher, and the vegetation period is longer in the south than in the north. For a detailed description of the study areas see Zedrosser et al. (in press).

The study populations differed in some demographic parameters (Sæther et al., 1998). Due to male biased juvenile dispersal (Støen et al., 2006) and low rates of male immigration from nearby areas, the numbers of adult males was low in the northern study area (Swenson et al., 2001; Swenson 2003). Illegal killing in the spring additionally reduced the number of adult males (Swenson et al., 2001; Swenson, 2003). As a result the number of adult males was stable but low during most of the study period. In the southern study area adult males were more abundant and some were killed on a regular basis by legal hunting (Swenson et al., 2001). Cub survival was significantly lower in the south, and Swenson et al. (1997; 2001) suggested that SSI was the main reason for this difference. Age of primiparity was 4.5 years

in the south and 5.4 years in the north. However, the ages of the mothers with their first successful litter were very similar in both study areas, 5.4 years in the north and 5.2 years in the south (Swenson et al., 2001).

Brown bears were immobilized from a helicopter in mid-April in the south and early May in the north, shortly after den emergence. 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 measure of overall size of an individual. Because all bears were captured within a 2-week period in each study area, we did not adjust head circumference for capture date. Head circumference was used as a measure of body size, because Derocher and Stirling (1998) suggested that head measurements rather than body length might provide the most useful measures to compare populations of polar bears. Few female bears were captured in the year they gave birth. To estimate their body size in this particular year, we used the study-area specific growth curves published in Zedrosser et al. (in press) to calculate their head circumference at primiparity.

In this study we only used female brown bears of known age (i.e. they were captured as yearlings with their radio-collared mother). We measured the reproductive success by counting the cubs of radio-collared females from the air or the ground three times during the year; just after leaving the natal den, at the end of the mating season, and just prior to entering the den in fall (September) or during capture of the female and her then yearling cubs in April/May the following year. Cub loss in the den was assumed when a lactating female was captured without cubs of the year. Based on observations in our study populations we define the pre-mating season as the time period after a bear had left the den until the second week of May, and the mating season as the time period from the third week of May until the first week of July (Dahle and Swenson, 2003). Brown bears rarely loose offspring during hibernation (Mano and Tsubota, 2002), thus yearling litter size represents an accurate measure of offspring surviving their natal year until hibernation.

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 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 the variables that 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 (Zedrosser et al., in press).

Individual population density index

The population density around each individual (within a radius of 17.84 km, which corresponds to the density of bears per 1000 km^2) was estimated in both the north and south, based on the high proportion of radio-collared 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-collared individual in our analysis was based on the location of individuals genetically identified by the scat sampling, the location of the radio-collared bears (71% of the radio-collared 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-collared (Swenson et al., 2001). We used the locations of radio-collared bears, a correction to include subadult males, and data on growth rate of the population to calculate an individual density index as in the south (Zedrosser et al., in press).

Male turnover

Since 1981, every hunter killing a bear in Scandinavia has had to report the sex and kill location and has to deliver a tooth for age determination, body measurements, and tissue samples to the authorities. To estimate the number of adult males killed in the vicinity of a given mother with cubs, we calculated the arithmetic center of the 95% minimum convex polygon (MCP) home range for every female with cubs. Within a radius of 40 km from this center we counted the number of adult males dying 1.5 years previously. This included males killed during the hunting season or for other reasons (i.e. accidents) and radio-collared males (arithmetic center of the 95% MCP home range) suspected to have been killed illegally. A 40-km radius was chosen, because 95% of all fathers of cubs in Scandinavia occurred within this radius from the mothers Bellemain et al. (2006). A time lag of 1.5 years was chosen, because Swenson et al. (1997) have shown that cub loss was highest 1.5 years after an adult male died. We defined a male as adult when ≥3 years, because the first age of male reproduction is 3 in

both study areas (Bellemain et al., 2006). The software package Ranges 6 (Anatrack Ltd., 52 Furzebrook Rd., Wareham, Dorset, UK) was used for home range calculation.

Statistical analyses

To evaluate differences in cub litter size between primiparous and multiparous females, we used generalized linear mixed models (GLMM); because several individuals were used more than once, we controlled for the effects of individual identity (McCullagh and Nelder, 1989; Steele and Hogg, 2003). The difference in yearling offspring body size of primiparous and multiparous mothers was also analyzed with a GLMM. The response variable was head circumference (in cm) of yearlings in a mother's litter, while controlling for random effects of maternal identity. The predictor variable was whether a mother was primiparous or multiparous while controlling for the factors reported by Dahle et al. (in press) to be important for yearling body size in the same populations (i.e.: maternal body size, litter size, sex of offspring, population density, cohort, study area). We analyzed if there was a difference in the probability of loosing cubs for primiparous and multiparous females with a GLMM. We chose "loss of one or more cubs" as the binary response variable, while controlling for the effects of study area.

The factors determining cub loss of primiparous females were identified using logistic regression (Hosmer and Lemeshow 2000). We chose "loss of one or more cubs" as the binary response variable. The following candidate predictors were available from 1987-2004: study area (south or north), male turnover (the number of adult male deaths in a radius of 40 km 1.5 years previously), age of primiparity of the female (4-7 years), body size of the female and the population density and environmental condition indices. We selected the best model in a backward elimination procedure.

Predictor variables were chosen according to their p-values; an α level of 0.05 was considered statistically significant, and an α level < 0.1 was considered statistically suggestive. The statistical software R 1.9.1 (R Development Core Team 2004) was used in all analyses.

RESULTS

We obtained ages of primiparity for 49 females, 19 in the north and 30 in the south (Table 1). However due to differences in data availability, the sample sizes differed among models. Only three females became primiparous in the northern area in the time period 2001-2004,

and we were either not able to reliably determine their age of first reproduction (2 cases) or not enough data were available for further analysis of cub loss (1 case).

The mean litter size of primiparous females (1.73 ± 0.78 (SD), N = 46) was significantly smaller than of multiparous females (2.42 ± 0.79, N = 170) (GLMM: β = -0.291, S.E. = 0.060, df = 139, t = 4.827, P ≤ 0.001, N = 216, number of groups = 76). The yearling offspring of primiparous females were significantly smaller than the yearlings of multiparous females, when controlling for other factors found to be important for yearling body size in these populations, i.e.: maternal body size, litter size, sex of offspring, population density, cohort, and study area (Dahle et al., in press) (GLMM: β = 1.180, S.E. = 0.549, d.f. = 146, t = 2.148, P = 0.003, number of groups = 49).

The temporal distribution of cub loss differed between the study areas. In the north cub loss only occurred in 2000, when 2 primiparous females lost cubs. In the south cub loss was evenly distributed through the entire study period; the only year without cub loss by a primiparous female was 1995. A binary model examining the probability of loosing one or more cubs (0 = no cub loss, 1 = loss of one or more cubs) showed that both primiparous and multiparous females had a significantly higher probability to lose cubs in the south than in the north (GLMM: β = 1.038, S.E. = 0.368, df = 66, t = 2.817, P = 0.006, N = 183, number of groups = 68). In the south primiparous females had a suggestively higher probability of cub loss than multiparous females (GLMM: β = -0.863, S.E. = 0.484, df = 83, t = -1.784, P = 0.078, N = 127, number of groups = 43). The proportion of cubs lost during different times of the year varied between ages and study areas, however primiparous females were not observed to loose cubs after the mating season in our sample (Table 2). A binary model examining the probability of loosing one or more cubs (0 = no cub loss, 1 = loss of one or more cubs) showed that, among primiparous females, there was a significant difference in the probability of loosing cubs between study areas and that the probability of cub loss was significantly and positively influenced by the number of males dying within 40 km 1.5 years previously (male turnover) (Table 3). There was a suggestive negative relationship between the probability of loosing one or more cubs and the age when the female was primiparous (Table 3). The other variables and interactions tested were not significant (age: β = -0.021, p = 0.976; condition index: β = -1.653, p = 0.227, population density: β = 0.059, p = 0.189).

DISCUSSION

We found that primiparous females had smaller litters of cubs and smaller yearling offspring than multiparous females. Both primiparous and multiparous females had a significantly

higher probability of cub loss in the south. A separate analysis of the southern area suggested that primiparous females had a higher probability of cub loss than multiparous females. The probability of cub loss of primiparous females increased with male turnover 1.5 years ago and suggestively decreased with age at primiparity.

As predicted, primiparous female brown bears had smaller litters than multiparous females (prediction 1). Patterns of lowered reproductive success by young and primiparous reproducers have been observed in birds (e.g.: Lack, 1966; Curio, 1983; Ollason and Dunnet, 1988) and mammals (e.g.: Clutton-Brock, 1988; 1991; Festa-Bianchet et al., 1995; Hellgren et al., 1995), including ursids (Craighead et al., 1974; 1995; Derocher and Stirling, 1994; Schwartz et al., 2003b, 2005). The causes for this lowered performance of primiparous individuals vary widely and can include (among others) physical maturation, lower reproductive experience and changes in dominance rank (Clutton-Brock, 1988). Female brown bears reach 90% of their asymptotic body size at approximately 4-5 years of age in Scandinavia (Zedrosser et al., in press), however they can continue to grow throughout life (Schwartz et al., 2003a). The smaller litter size at primiparity in brown bears therefore may be due to age-related changes in allocation of energy to growth and reproduction. This trade off also seems to involve offspring body size, because, as predicted, the average yearling head circumference of offspring of primiparous females was smaller than the average yearling body size of multiparous females (prediction 2). Dahle et al. (in press) found that body size and mass of yearling brown bears were positively related to maternal size. Our results of a lower performance of primiparous mothers are also supported by results from the closely related polar bear (*Ursus maritimus*), where offspring size was affected by maternal age and mass (Derocher and Stirling, 1994). This also has been found in ungulates (Clutton-Brock, 1991; Festa-Bianchet et al., 1995).

As predicted, a mother looses more offspring when primiparous than when multiparous (prediction 3). Although the offspring of primiparous mothers were smaller, this higher probability of loss was most likely not related to a lower energetic investment of primiparous mothers into their offspring. This is indicated by the differences in cub loss between the study areas. In the north, both primiparous and multiparous females rarely lost cubs (Swenson et al., 1997; 2001; Swenson 2003). However in the south, both primiparous and multiparous females lost significantly more cubs than in the north, and primiparous females lost suggestively more cubs than multiparous females. As predicted, we found that the probability of cub loss of primiparous females was positively correlated to male turnover (prediction 4a), and suggestively negatively correlated to female age at primiparity (prediction 4b). Contrary to

our predictions, the probability of cub loss was not related to environmental conditions or the body size of primiparous females. Population density did not influence cub loss.

Several factors have been proposed as important for bear cub survival (McLellan 2005; Miller et al., 2003; Swenson et al., 1997; 2001). Our results showed large differences in cub mortality rates and annual mortality patterns between the study areas (Fig 1), but male turnover was the most important factor explaining cub loss of primiparous females. This suggests that SSI is the major mortality factor for cubs of primiparous females. The timing of cub loss also supports this, because most primiparous females lost their cubs during the mating season (Table 2). According to the SSI-hypothesis, an infanticidal male should not kill his own young (Hrdy, 1979). This has been confirmed in brown bears in the south (Bellemain et al., 2006). The correlation between male turnover and cub mortality has been reported from the south earlier for all females combined (Swenson et al., 1997; 2001). Our results show that primiparous mothers lose more cubs than multiparous females, which suggests that primiparous mothers are less experienced or efficient in defending their cubs against infanticidal males.

McLellan (2005) has proposed two alternative mechanisms to explain how SSI may operate in brown bears. The "immigrant male hypothesis" (McLellan 2005) predicts that the death of adult males would likely promote the influx of immigrating males and/or possibly realignment of the home ranges of adult males. This would result in males coming into contact with litters that they did not father and thus they should kill the dependent offspring to create mating opportunities (McLellan, 2005; Swenson, 2003). The "mate recognition hypothesis" (McLellan, 2005) predicts that any male, including adult resident males, should kill cubs to gain breeding opportunities with the mother. In the north, high initial mortality of adult males and low male immigration rates, apparently due to illegal killing, kept numbers of adult males low (1-3 males) in the north until 1996. Then recruitment of locally produced young males and probably increased immigration from the increasing population from nearby areas increased the number of males by 3-4 times (Swenson et al. 2001; Swenson JE, unpublished). This probably has resulted in increased loss of cubs with primiparous mothers due to SSI in the north at the end of our study period. The situation in the northern study area would be more consistent with the immigrant male hypothesis. However, in the southern study area with higher male densities, cub loss has been consistently high in the entire study period (Swenson et al. 1997; 2001). Killing of adult males was followed by an increase in cub mortality 1.5 years later (Swenson et al. 1997; 2001), and Bellemain et al., (2006b) have suggested that mainly resident males are responsible for killing dependent offspring. This

situation may be more consistent with the mate recognition hypothesis, as suggested by McLellan (2005). However we were unable to specifically test these proposed hypotheses, because the necessary data were not available.

The probability of cub loss of primiparous females was suggestively negatively correlated to female age at primiparity. Our results suggest that females that are primiparous at age 4 lost cubs most often (Table 2). Only females in the south reached primiparity at this age, but the ages of the mothers when giving birth to their first successful litter were very similar in both study areas (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. It is unclear why females primiparous at age 4 have a higher probability of cub loss. Only females primiparous at 4 years lost cubs in the pre-mating season, but the majority of cubs lost by primiparous 4-year-olds occurred during the mating season (Table 2). This seemed not to be related to body size or environmental conditions, because neither of these factors influenced the probability of cub loss. In addition, observations in more southern parts of Europe show that females can successfully raise cubs already at age 3 (Frkovič et al., 2001; Zedrosser et al., 2004). First-time breeders may lack refined behavioral skills associated with foraging and parental care (Becker et al., 1998; Wang and Novak, 1994). The high proportion of cubs of 4 year-olds lost during the mating season suggests that, in a population where SSI is a major source of cub mortality, an additional year of experience with other bears increases a young female's chance of successfully raising a litter. An additional year of experience may provide a better knowledge of local dominance hierarchies or more experience in avoiding potentially infanticidal individuals. From the point of view of lifetime reproductive success, it may be advantageous for young female brown bears to reproduce as early as possible, because male turnover is unpredictable in space and time.

Differences in the reproductive performance of primiparous and multiparous mothers seem to be independent of environmental conditions. The major cause of cub loss of primiparous females seems to be SSI, which should be independent of environmental conditions, as has also been found by Swenson et al. (2001). In contrast, Miller et al. (2003) suggested that variations in brown bear cub survivorship may be influenced by local environmental factors in Alaska. Experimental evidence in birds suggests that age-specific reproductive success is independent of environmental effects (Daunt et al., 1999). In our study, there was almost no cub loss in the north, whereas cub loss in the south was evenly distributed through the entire study period (Fig 1). This strongly suggests that the differences

in cub mortality of primiparous females between our study areas must be independent of environmental fluctuations.

The importance of SSI in brown bear populations remains under debate among biologists (e.g.: McLellan, 1994; 2005; Miller et al., 2003; Swenson et al., 1997; 2001; Wielgus and Bunnell, 2000). While researchers in Europe have found support for the SSI-hypothesis (Swenson et al., 1997; 2001), results from North America are not as clear (McLellan 2005; Miller et al., 2003; Wielgus and Bunnell, 2000). A possible explanation for some of these differences may be the higher age of primiparity in North America, because our results suggest that females being primiparous at older ages lose fewer cubs.

We conclude that cub loss of primiparous female is related to SSI, a pattern that has been confirmed before for females generally in Scandinavia (Swenson et al., 1997; 2001). In areas without SSI (north), primiparous females rarely seem to loose cubs, whereas in areas with SSI (south), cub loss by primiparous females was high. Primiparous mothers loose more offspring than multiparous mothers, which suggests that they are less able/experienced in defending their offspring. Because cub loss in primiparous females was not related to environmental conditions, their body size or population density, SSI seems to be a more important agent of cub mortality for primiparous than multiparous females. In general, females in the south were primiparous earlier than females in the north, however the ages of first successful litter were the same in both areas. We found suggestive evidence that females primiparious at age 4 in the southern study area had the highest probability of cub loss, maybe due to lack of experience with other bears. The probability of cub loss of primiparous females was not related to environmental conditions, their body size or population density.

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Table 1

Mean age of first reproduction and proportion of female brown bears first giving birth at a given age in two study areas in Scandinavia in 1987-2004. SE = Standard error, N = sample size.

Study area	Mean age of primiparity (± SE)	4 years	5 years	6 years	7 years	N
South	4.53± 0.63	0.53	0.4	0.07	0	30
North	5.43 ± 0.87	0.05	0.68	0.21	0.05	19

Table 2

Timing of cub loss in relation to age at primiparity for primiparous female brown bears in two study areas in Scandinavia in 1987-2004. The pre-mating season is the time period from leaving the den until the second week of May; the mating season is the time period from the third week of May until the first week of July. Primiparous females were not observed loosing cubs outside these two time-periods. The proportion is given in parentheses, N = sample size.

Study area	Age at primiparity	Timing of cub loss		No loss	N
		Pre-mating season	Mating season		
South	4	3 (0.27)	7 (0.64)	1 (0.09)	11
	5	-	5 (0.50)	5 (0.50)	10
	6	-	1 (0.33)	2 (0.66)	3
North	5	-	2 (0.28)	11 (0.72)	13

Table 3

Probability that a primiparous female brown bear lost at least on cub from a litter in two study areas in south-central and northern Sweden from 1987-2004. The binary response variable was the probability of "loss of one or more cubs". The predictor variables available were study area (south or north), male turnover (the number of adult male deaths in a radius of 40 km 1.5 years previously), age at primiparity, body size at primiparity, and environmental conditions, while controlling for population density (N: South = 24; North = 13). Only significant ($p \leq 0.05$) and suggestive ($p \leq 0.1$) predictors are shown.

Variable		β	S. E.	df	p
Study area					
	South	0	0		
	North	-2.465	1.113	1	0.027
Male turnover		1.506	0.755	1	0.046
Age at primiparity		-1.639	0.909	1	0.071

Paper VII

"The process of maturation is slow, continuous and obscure." –
R. Rappart, "Ecology, Meaning and Religion."

Socially induced delayed primiparity in brown bears *Ursus arctos*

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Abstract

Reproductive suppression through behavioural 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 (*Ursus arctos*) females form matrilinear assemblages with related females using a common and largely exclusive area. Behavioural 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 will reproduce earlier than philopatric females. The average age of primiparity was 4.3 years in females that dispersed outside their mother's home range (n=8) and 5.2 years in philopatric females (n=10). 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.

Key words: maturity, reproduction, reproductive success, reproductive suppression, social organization

Introduction

Costs and benefits of dispersal or philopatry to young animals may vary due to differences in mortality, access to unrelated mates, possibility to find suitable offspring rearing space, familiarity with the local area and neighbours or benefits of kin selection, and suppression by dominant animals (see Wiggett and Boag 1990). 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 typically involves behavioural or physiological means (Wasser and Barash 1983, Brant et al. 1998, Clarke et al. 2001, Solomon et al. 2001, Hackländer et al. 2003). Reproductive suppression is common in group-living mammals, but to our knowledge this has not yet been shown in wild large carnivores other than those with well-developed social organization (e.g. wolves *Canis lupus*, see Mech 1970, African wild dogs *Lycaon pictus* and Ethiopian wolves *Canis simensis*, see Creel and MacDonald 1995).

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). Reproductive suppression in a young female can be adaptive if withholding reproductive effort will increase later reproductive success sufficiently to compensate for delayed primiparity (Wasser and Barash 1983, Wolff 1997).

The brown bear (*Ursus arctos*) is a large carnivore with a promiscuous mating system (Pasitschniak-Arts 1993, Schwartz et al. 2003, Bellemain et al. 2006). Natal dispersal is sex-biased, with males generally dispersing and philopatric females (Glenn and Miller 1980, Blanchard and Knight 1991, McLellan and Hovey 2001, Proctor et al. 2004). Both the probability of natal dispersal and natal dispersal distances are inversely density dependent (Støen et al. 2006). Among adults, males have larger home ranges than females, but both males and females have intra- and inter-sexually overlapping ranges (Pasitschniak-Arts 1993, Dahle and Swenson 2003a).

Brown bears are generally not considered to be territorial (Pasitschniak-Arts 1993, Schwartz et al. 2003), but dominance hierarchies have been observed (Pulliainen et al. 1983), especially when bears aggregate at garbage dumps and at salmon (*Oncorhyncus* spp.) spawning streams (see IGBC 1987 for a review, Craighead et al. 1995, 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.

After their near extirpation around 1930, the Scandinavian brown bear population increased in numbers and expanded in range from four small remnant areas. Today it encompasses more than half of Sweden and parts of Norway (Swenson et al. 1994, 1995). This expansion in range, with both philopatric and dispersed females in the same geographical area (Swenson et al. 1998, Støen et al. 2006), provided us with a rare possibility to test whether young philopatric females are reproductively suppressed.

In this study we examined whether dispersal status (philopatric or dispersed) influenced age of primiparity. In mammals, body size, body mass and population density may also influence sexual maturity (Festa-Bianchet et al. 1995, 1998, Svendsen and White 1997, Forchhammer et al. 2001, Bonenfant et al. 2002, Weladji et al. 2003, Neuhaus et al. 2004); thus we controlled for these variables in our analysis. Based on the recent finding of matrilinear assemblages in brown bears (Støen et al. 2005), we predict that dispersed females relieved from matrilineal influence will reproduce earlier than philopatric females. Because the home ranges of adult male brown bears can overlap with their daughters and provide a potential risk of inbreeding (McLellan and Hovey 2001, Dahle and Swenson 2003a, Bellemain et al. 2006), we predict that females relieved from paternal influence by dispersing outside their father's home range will reproduce earlier than females living within their father's home range.

Methods

Study area, home range estimations and dispersal status

The study area was in Dalarna and Gävleborg counties in south-central Sweden and Hedmark County in southeastern Norway (61º N, 18º E). The rolling landscape in this region is covered with coniferous forest, dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). During 1986-2003 we captured, radiomarked and monitored 32 adult female bears that weaned 78 litters with 175 yearlings. Eighteen yearling daughters from 7 different females were successfully followed until primiparity. The fathers of the yearlings were determined from DNA analysis of shot and captured males (Bellemain 2004). We located the bears approximately once a week during their active period for several years, using standard triangulation methods from the ground or from the air (Dahle and Swenson 2003a). The study area and the methods used to capture, collar and radiotrack bears are described by Dahle and Swenson (2003a, b) and Arnemo et al. (2006).

A daughter was defined as a natal disperser if she left her natal area and was never again observed within her natal area or her mother's multiannual home range after separation. Daughters that were always or periodically observed within their natal areas or their mother's multiannual home range after separation were defined as philopatric. Natal areas were estimated as 95% minimum convex polygons (MCP), using the mother's locations with the Ranges 6 computer package (Anatrack Ltd., 52 Furzebrook Rd., Wareham, Dorset, UK). A 95% MCP estimate was used to avoid the influence of unusual forays and because MCP estimates are the most frequent home range estimators reported in the brown bear literature (Schwartz et al. 2003). Family break-up normally occurs in the spring (May-June) when cubs are aged 17-18 months (Dahle and Swenson 2003b). An underestimation of the size of a natal area could overestimate the number of dispersers using this criterion. We therefore estimated the natal areas (95% MCP) based on all of the mother's locations during the first two years of the daughter's life and not only from the positions when the daughter accompanied the mother. This was done for two reasons: a) relatively few locations were obtained annually for each litter, and b) a 95% MCP can underestimate the home range size of brown bears when using few locations (Macdonald et al. 1980). By including all of the mother's positions in the second year of her daughter's life, we obtained a more reasonable estimate of the home range that the mother used while accompanied by cubs, i.e. the natal area. The average number of locations used to

estimate 18 natal areas was 58 ± 13 (mean ± SD, range: 28 - 76). To reduce autocorrelation, only locations separated by at least 100 h were used, which corresponds to the minimum time between successive locations of the bears (Dahle and Swenson 2003b). The use of multiannual home ranges is also justified because adult females have high fidelity to their home range in successive years (Støen et al. 2005).

The multiannual home ranges (95% MCP) were estimated differently for mother-daughter dyads of philopatric and natal dispersers. The multiannual home ranges of mothers of philopatric daughters were estimated using locations of the mother obtained in all the years from the time the daughter turned 2 years until (and including) the year of the daughter's first reproduction. An inclusion of the mother's positions in the years when the dispersing daughter resided in the natal area would bias the multiannual area of the mother towards the natal area and thus overestimate the number of dispersers. Multiannual home ranges of mothers with dispersing daughters were therefore estimated from locations obtained during the first years the daughter was not observed within the natal area until (and including) the year of her first reproduction.

The average number of locations used to estimate the multiannual home ranges of mothers with philopatric daughters ($n = 10$) was 121 ± 50 (mean ± SD, range: 26 - 185). The corresponding annual number of locations of their philopatric daughters these years ($n = 42$) was 31 ± 10 (range: 9 - 47). The mother of one disperser lost her radio collar prior to separation. The average number of locations used to estimate the multiannual home ranges of the other mothers with dispersing daughters ($n = 7$) was 61 ± 42 (range: 26 - 144). The corresponding annual number of locations of their daughters after natal dispersal these years ($n = 16$) was 31 ± 10 (range: 4 - 43).

The spatial association between a young female and her father was estimated based on locations of the daughter within the father's multiannual home range after weaning. The multiannual home ranges of fathers (95% MCP) were estimated using locations of the father obtained in all the years from the time the daughter turned 2 years until (and including) the year of the daughter's first reproduction. The average number of locations used to estimate the multiannual home ranges of 11 fathers was 96 ± 43 (range: 22 - 184). The corresponding annual number of locations of their daughters these years ($n = 38$) was 29 ± 11 (range: 4 - 47).

Monitoring of reproduction

The reproductive status of daughters was determined by three methods; direct observations, live capture, and visits to den sites. We observed a family as soon as possible after it left the den, again around the end of the mating season in late June-early July, and again before they entered the den in the autumn. Immobilised daughters without cubs of the year were checked for lactation by signs of nursing (e.g., presence of milk in the udder). We visited dens to determine whether young had been present outside the den, based on tracks and markings from their climbing in nearby trees. A daughter was considered to have reproduced if she was observed with cubs, if she was lactating when captured soon after emerging from the den, or if tracks of small cubs were found at the den site. If none of these criteria were confirmed, she was considered to not have reproduced.

Body size measurement

The head circumference (at the widest part of the zygomatic arch between eyes and ears) was measured with a tape and used as a measure of the overall body size of an individual (Zedrosser et al. in press). Derocher and Stirling (1998) suggested that head measurements may be more useful than body length to compare body size in different populations of polar bears (*Ursus maritimus*). Live weight was measured with a scale. Because all bears were captured within a 2-week period each year (late April), we did not adjust body size or body mass for capture date. Growth was measured as the kilograms of body mass gained and as cm of head circumference gained from 1 to 4 years of age.

Individual population density index

A population size estimate, based on a DNA analysis of non-invasive sampling of scats, was carried out in the study area in 2001 and 2002 (Bellemain et al. 2004). 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 of the center of the focal bear's home range (which corresponds to the density of bears per 1000 km^2), based on the centers of the locations of all scat samples for each individual (Zedroser et al. in press). Bellemain (2004) found that 71% of all radio-collared bears in the 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 (Zedrosser et al. in press). Sæther et al. (1998) estimated a population growth rate of about 16% annually in the study area for the period 1985-1995. Population size and density estimates based on aerial capture-mark-recapture techniques were carried out in the 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 (see Zedrosser et al. in press for a more detailed description).

Statistical analysis

We fitted quasi-Poisson regression models for age of primiparity, using the glm function in R (the MASS library) (R Development Core Team 2005). The variables of interest were dispersal status (philopatric or dispersed), head circumference, body mass and the individual population density index. All the variables used in the models were measured at the same age of the bears. In our initial model we chose 4 years of age, because this is the lowest age of first reproduction recorded in Scandinavian female brown bears (Sæther et al. 1997), and it gave the largest sample size. We used both head circumference and body mass in our models, because head circumference gives a measure of structural size, whereas body mass also reflects variations in body condition and thus environmental conditions.

Results

Ten daughters were located within their natal area or within their mother's multiannual home range every year after separation, including the year when they had their first litters, and were defined as philopatric. Eight daughters left their natal area and were never again observed within it, including the year of primiparity, and were defined as dispersers. The mean age of dispersal was 2.25 ± 0.89 (mean $\pm$ SD, range: $1 - 3$) years, or a minimum of 1 year and an average of 2 years before primiparity.

The mother of one natal disperser used in the analysis lost her radio collar prior to separation and could possibly have overlapped with her dispersed daughter in the years after separation, if she had shifted her home range along with the daughter. In the year of primiparity (5 years old), the dispersed daughter's closest position was 52 km from the border of her natal area, whereas the mother was shot 4 years later within the natal area. The 7 other dispersing daughters were never observed within their mothers' multiannual home ranges after leaving the natal area.

The average age of primiparity of all daughters was 4.8 ± 0.7 years, and as 4-year-olds their average head circumference was 56.0 ± 2.2 cm, body mass was 77.9 ± 10.4 kg and the average individual population density index was 31.6 ± 18.4 bears/1000 km^2. Age of primiparity was the only variable that was significantly different between philopatric and dispersed daughters (Table 1). When controlling for head circumference, body mass and density when 4 years old, a generalized linear model (GLM) revealed that dispersal status was the only variable affecting age of primiparity (Table 2). Emigrant daughters started to breed at a mean age of 4.3 years, philopatric daughters started at a mean age of 5.2 years (Table 1).

Lactation is energetically costly (Farley and Robbins 1995, Hilderbrand et al. 2000). Because 7 (87.5%) of the 9 daughters that gave birth as 4-years-olds had dispersed, measuring head circumference and body mass approximately 4 months after parturition could bias our data towards smaller sizes of dispersing daughters. However, when using head circumference, mass and individual population density index values of 14 of the daughters when they were measured as 3 year olds in a GLM model, dispersal status remained the only variable having a significant effect on age of primiparity (Table 2).

Growth rate and nourishment as young affect primiparity in several species (Reiter and LeBoef 1991, Svendsen and White 1997, Hofer and East 2003; Weladji et al. 2003). However, there was no effect of yearling head circumference or body mass ($\beta = -0.009$, p = 0.160, df = 14 and $\beta = -0.011$, p = 0. 477, df = 15, respectively) and growth in head circumference or body mass from 1 to 4 years of age ($\beta = -0.002$, p = 0.504, df = 14 and $\beta = 0.002$, p = 0.887, df = 15, respectively) on age of primiparity, when controlling for natal dispersal status in the GLM models.

The individual population density index did not differ significantly between the natal area (31.8 ± 16.3) and the area where the daughters (n = 18) gave birth to their first litter (31.8 ± 19.5, t = 0.002, p = 0.999). This was true both for philopatric

daughters where the population density index was 32.4 ± 15.3 in the natal area and
37.2 ± 22.5 in the area where they gave birth to their first litter, (n = 10, t = 1.206, p =
0.258) and dispersing daughters where the population density index was 31.0 ± 18.5
in the natal area and 24.9 ± 13.4 in the area where they gave birth to their first litter,
(n = 8, t = 1.208, p = 0.266). Some daughters had their first litter when older than 4
years (n = 9), but their individual population density index did not differ between the
area they resided in as 4-year-olds (39.0 ±20.8, used in the GLM model) and the area
where they had their first litter (39.2 ±22.8, t = 0.083, p = 0.94).

We obtained multiannual home ranges of the fathers of 11 daughters. Five of
these daughters did not have locations within their fathers multiannual home range at
least 1 year before primiparity. The other 6 daughters were located within their
father's home range every year until primiparity. There was no difference in the age
of primiparity between these two groups of females (GLM, $\beta = 0.057$, p = 0.665, df =
6), when controlling for head circumference ($\beta = 0.033$, p = 0.450), body mass ($\beta =
0.005$, p = 0.571) and density ($\beta = 0.005$, p = 0.272) when 4 years old.

Discussion

As predicted, philopatry was associated with an increased age of primiparity. Only
dispersal status was significant in the GLM, which suggests a social suppression of
reproduction of philopatric daughters residing within their mother's home range
(Table 2). Reproductive suppression of young females has been shown in several
gregarious species but, to our knowledge, this is the first time socially induced
delayed primiparity has been documented in a large non-gregarious wild carnivore.
Dalerum et al. (in press) found that reproductive failure in captive female wolverines
(*Gulo gulo*) kept in a highly aggregated social environment was related to low social
rank. Social tendencies and physiological mechanisms mediating this reproductive
suppression may be viewed as reaction norms to the social environment in wolverines,
indicating that the social flexibility of solitary carnivores might be greater than
commonly observed (Dalerum et al, in press).

The reasons for reproductive suppression in brown bears, similarly to many
gregarious species, could include inbreeding avoidance (Wolff 1992) or to minimize
resource competition (Wasser and Barash 1983). Reproductive suppression as an
inbreeding avoidance mechanism has been observed in several species, and occurs
when subadult females remain in contact with male relatives and are not exposed to

unrelated adult males (Wolff 1992, Lambin 1994, Clarke et al. 2001, Clark and Galef 2001, 2002). Contrary to our prediction there was 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; however, due to the low sample size in our study we can not rule out the importance of the father's influence. Because of the low risk of inbreeding shown by theoretical modelling (McLellan & Hovey 2001) and empirical data showing only 2% incestuous matings (reproduction between daughter and father) (Bellemain et al. 2006), we believe that fathers probably have little influence on female primiparity in brown bears. In addition, extensive home range overlap among adult males and a promiscuous mating system, as shown by frequent occurrence of multi-paternal litters (Bellemain et al. 2005) indicate frequent exposure of young females to unrelated males. Frequent exposure of young females to unrelated males may counteract potential reproductive suppression from related males (McGuire and Getz 1991, Sillero-Zubiri et al. 1996).

Due to the extensive overlap 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). 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.

Even if female brown bears in our study area reach 90% of asymptotic size at a mean age of 4.1 years (Zedrosser et al. in press), brown bears may continue to grow throughout their life (Schwartz et al. 2003). Dominance hierarchies have been related to size in brown bears (Craighead et al. 1995). We suggest that the increased size with age may improve the status of subdominant females within a hierarchy, which again reduces the threat of infanticide and probably increases the possibility for successfully rearing offspring.

The nutritional condition of females has been found to be important for the onset of reproduction in brown bear populations (Stringham 1980, 1990; Bunnel and Tait 1981), and several other mammals (Svendsen and White 1997, Weladji et al. 2003, Neuhaus et al. 2004). Neither head circumference nor body mass as yearlings, 3-year-olds and 4-year-olds influenced age of primiparity in our GLM models. The reason might be because small Scandinavian brown bear females show compensatory growth (Zedrosser et al. in press), and thus may not have a disadvantage of small body size when reaching reproductive age. Growth rate has been reported to influence the age of primiparity in spotted hyenas (Hofer and East 2003), however, we did not find this in brown bear females, because there was no effect on age of primiparity when controlling for natal dispersal status in our GLM models.

Population density, which has been found to be important for age of primiparity in several mammalian species (Festa-Bianchet et al 1995, 1998, Forchhammer et al. 2001, Bonenfant 2002), did not appear to influence the age of primiparity within the range of densities observed in our study area. The individual density indices did not differ in the natal area and in the area where the dispersing daughters had their first litter. This suggests that dispersing females settled in a vacant area rather than in an area with generally fewer bears. This result suggests the inference that it is the related females that suppress reproduction and not bear density per se.

One reason why some females may not disperse even if being philopatric delays first reproduction may be that dispersal is determined by factors other than the delay in reproduction due to reproductive suppression. In Scandinavia 60% of female bears do not disperse and brown bear natal dispersal is inversely density dependent (Støen et al. 2006). In North America female dispersal is rare (McLellan and Hovey 2001). There may be a fitness advantage of philopatry, such as improved survival of the female or her cubs, familiarity with the local area and neighbours, 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 behaviour in brown bears.

Acknowledgements

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Table 1. Age of primiparity, body size (head circumference), body mass (live weight) and individual population density index (density) for philopatric and natal dispersed female brown bears in Scandinavia.

	Philopatric daughters			Dispersed daughters				
	X	*SD*	*n*	*X*	*SD*	*n*	*t**	*P*
Age of primiparity (years)	5.2	0.6	10	4.3	0.5	8	3.547	0.003
Head circumference (cm)								
1 year old	39.4	2.2	10	40.3	2.0	6	0.886	0.394
3 years old	51.6	1.8	8	52.3	2.7	6	0.646	0.530
4 years old	55.8	2.5	10	56.4	1.9	8	0.537	0.599
Growth 1-4 years age	16.4	2.4	10	16.2	3.1	6	0.160	0.877
Live weight (kg)								
1 year old	21.3	4.9	9	22.3	2.5	6	0.516	0.615
3 years old	57.4	8.3	8	60.8	7.6	6	0.781	0.450
4 years old	76.4	12.7	10	79.8	7.0	8	0.677	0.508
Growth 1-4 years age	54.2	9.6	9	58.7	8.6	6	0.935	0.369
Density (bears/1000 km^2)								
Natal area	32.4	15.3	10	31.0	18.5	8	0.182	0.858
3 years old	41.5	21.0	8	28.5	13.4	6	1.328	0.209
4 years old	36.0	21.1	10	26.1	13.6	8	1.143	0.270
First litter	37.2	22.5	10	24.9	13.4	8	1.363	0.192

* Two-sample t test.

Table 2. Generalized linear model of the effects of natal dispersal status (philopatric or dispersed), body size (head circumference), body mass (live weight) and individual population density index (density) when 3 years of age (n = 14) and 4 years of age (n = 18), on the age of primiparity in female brown bears in Scandinavia 1986-2003.

Explanatory variables	β	SE	*df*	*t*	*P*
3 years old					
Density (bear/1000km^2)	0.0009	0.0027	9	-0.320	0.756
Head circumference (cm)	0.0316	0.0218	10	1.452	0.177
Live weight (kg)	-0.0055	0.0044	11	-1.271	0.230
Natal dispersal status (Philopatric vs Dispersed)	-0.1678	0.0675	12	-3.488	0.029
4 years old					
Density (bear/1000km^2)	0.0009	0.0018	13	0.507	0.620
Head circumference (cm)	0.0267	0.0235	14	1.141	0.273
Live weight (kg)	-0.0033	0.0026	15	-1.269	0.224
Natal dispersal status (Philopatric vs Dispersed)	-0.2017	0.0564	16	-3.579	0.002

The models were run repeatedly after successively excluding the least significant term, until the models included only significant terms.

Paper VIII

"Evolution is cleverer than you are!" – Francis Crick

Human-induced life history changes promote conservation of brown bears

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Human-induced selection due to harvesting is a potentially negative consequence of exploiting fish and wildlife populations. Human-induced selection of life-history traits has been documented in commercially exploited fisheries populations[1-4], but in large mammals, effects have only been documented regarding phenotypic traits[5,6]. We report an apparent case of human-induced life-history change in brown bears (*Ursus arctos*). Populations with a long history (>50 generations) of human persecution show a greater and earlier reproductive investment than populations with a short history (<15 generations). The populations with long exploitation include the world's most productive[7], which probably explains why many have responded more positively to recent changes in management than most populations with short exploitation (North America)[8,9].

Phenotypic evolution is probably occurring in exploited populations as a result of selective harvesting, although the genetic basis for such changes has rarely been demonstrated[10]. Selective phenotype-based harvest of high-quality rams of bighorn sheep (*Ovis canadensis*) over 5 generations resulted in a depletion of genes that conferred rapid early body and horn growth[6] and several authors have warned of potential selective effects of sport harvest of individuals with large horns or antlers[6,11,12]. Although the heritability of life-history traits is much lower than that of morphological traits[13], it is large enough to bring about genetic change under selective exploitation[10]. Experimental size-selective harvesting of fish populations has shown evolutionary effects on somatic growth and population productivity[3] and life-history traits of fish can change rapidly when under strong selection[14].

We examined whether long-term heavy exploitation of brown bear populations resulted in selective changes in life-history strategies. Because life-history strategies often involve trade-offs between body growth and reproduction, life-history theory predicts that animals in populations with a high adult mortality rate should prioritize reproduction over body growth in order to increase the probability of reproducing before death[14].

The duration of persecution of brown bears by humans differed between Europe compared with North America and northern Asia. To reduce depredation by bears, extermination efforts in Europe were carried out for centuries with primitive weapons and traps, and populations declined relatively slowly until effective firearms became available in the 1800s[16-18]. In North America the distribution of brown bears

south of Canada collapsed rapidly from 1850-1920 and most of the remnant, populations disappeared from 1920-70 as a consequence of persecution by settlers with modern weapons[19]. In much of northern North America and Asia, settlers arrived later and in smaller numbers, and brown bear populations have remained large over large areas[8].

We used a linear model to analyze the relative degree of reproductive investment (i.e. litter size while controlling for female mass) in 6 populations that experienced long persecution in Europe (>500 years or >50 generations, with a ~10-year generation length[20,21] with 22 populations with a short period of persecution (<150 years or <15 generations) in North America, northern Japan and central Siberia. By using mean adult female body mass, we also addressed habitat quality differences, including diet (% meat) and population density, because these factors are intercorrelated[22]. Because persecution time is related to continent, we evaluated the 6 mitochondrial DNA lineages the populations belonged to[23-25]; one lineage stretches from northern Europe through Asia to Canada. Also, we evaluated the effect of sympatry with black bears (*Ursus americanus, U. thibetanus*), because they have been suggested to compete with brown bears[26].

Brown bears with a long history of persecution produced significantly more offspring for their body mass than those with a short history (Fig. 1). The significant response variables explaining mean litter size were length of persecution ($\beta_{persecution}$ = 0.51 , s.e.m. = 0.11, t_{27} = 4.76, P < 0.00001) and mean adult female body mass ($\beta_{female\ mass}$ = 0.004 , s.e.m. = 0.001, t_{27} = 4.46, P = 0.0002). No significant effect was found for the presence of black bears ($\beta_{black\ bears}$ = -0.11 , s.e.m. = 0.08, t_{27} = -1.43, P = 0.17) nor the mitochondrial DNA lineage ($\beta_{lineage}$ = 0.005 , s.e.m. = 0.03, t_{27} = 0.89, P = 0.85).

In addition, females in populations with long persecution reproduced earlier in relation to their body mass than those with short persecution. Female brown bears in 3 interior North American and 2 Scandinavian populations at the same latitudes in the boreal forest reach 90% of their asymptotic size, when reproduction generally starts in mammals[27], at approximately the same age (3.8-4.8 years vs. 4.1-4.7 years, respectively). However, North American females need 1.3-1.7 years longer to reach their 90% asymptotic mass (7.2-7.9 years vs. 5.9 years, respectively)[28-30]. In North America primiparity was at 6-8 years, about at 90% asymptotic mass and after 90%

body size[28]. However primiparity occurs at 4.5-5.4 years in Scandinavia[31], which coincides with 90% asymptotic size, but is before 90% asymptotic mass.

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 and earlier in reproduction in relation to body mass. As a result, the highest documented reproductive rates for brown bears are from these populations[7]. This adaptation has probably allowed the species to more easily survive persecution and even increase with enlightened management in many human-dominated landscapes of Europe[9,18], in contrast to North American brown/grizzly bears, with lower reproductive rates[8]. Behavioral traits may also have been subject to human selection, because European brown bears are less aggressive to humans[32,33] and less diurnal[34] than North American bears, which also make them easier for humans to tolerate.

Material and methods

We collected data from 28 different brown bear populations in North America, Asia and Europe. In our own study populations (northern and southern Sweden) body weights were estimated by averaging spring weights of adult ($\geq$ 5 years) females captured in the course of our study. All other data were obtained from the literature or by personal communication (Table 1). In populations where bears were weighed only in spring, the mean spring weights were multiplied by 1.28, which is the average seasonal increase exhibited in populations were bears were weighed in both spring and autumn[35]. Statistical analyses were carried out in R 1.9.0.

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Figure 1 Relationship between mean adult female mass and mean litter size for brown bears from 28 populations from Europe, North America and Asia. The solid lines represent the regression lines, dotted lines the 95% confidence interval. Upper case letters indicate North American (NA) and Asian (AS) populations (A = Admirality Island/ NA, B = Alaska Penninsula/ NA, C = Alaska Range/ NA, D = Black Lake/ NA, E = East Front Montana/ NA, F = Eastern Brooks Range/ NA, G = Flathead/ NA, H = Katmai National Park/ NA, I = Kenai Penninsula/ NA, J = Kodiak island/ NA, L = MacKenzie Mountains/ NA, M = McNeil Sanctuary/ NA, N = Nelchina/ NA, O = Northcentral Alaska Range/ NA, P = Northern Yukon/ NA, Q = Southern Hokkaido/AS, R = Susitna Valley/ NA, T = Western Brooks Range/ NA, S = Toktoyaktuk/NA, U = Yakutia/AS, V = Yellowstone National Park/ NA); lower case letters indicate European populations (a = Dinara Mountains, b = Leningrad Oblast, c = Northern Sweden, d = Southern Finland, e = Southern Sweden, f = Western Cantabrian Mountains).
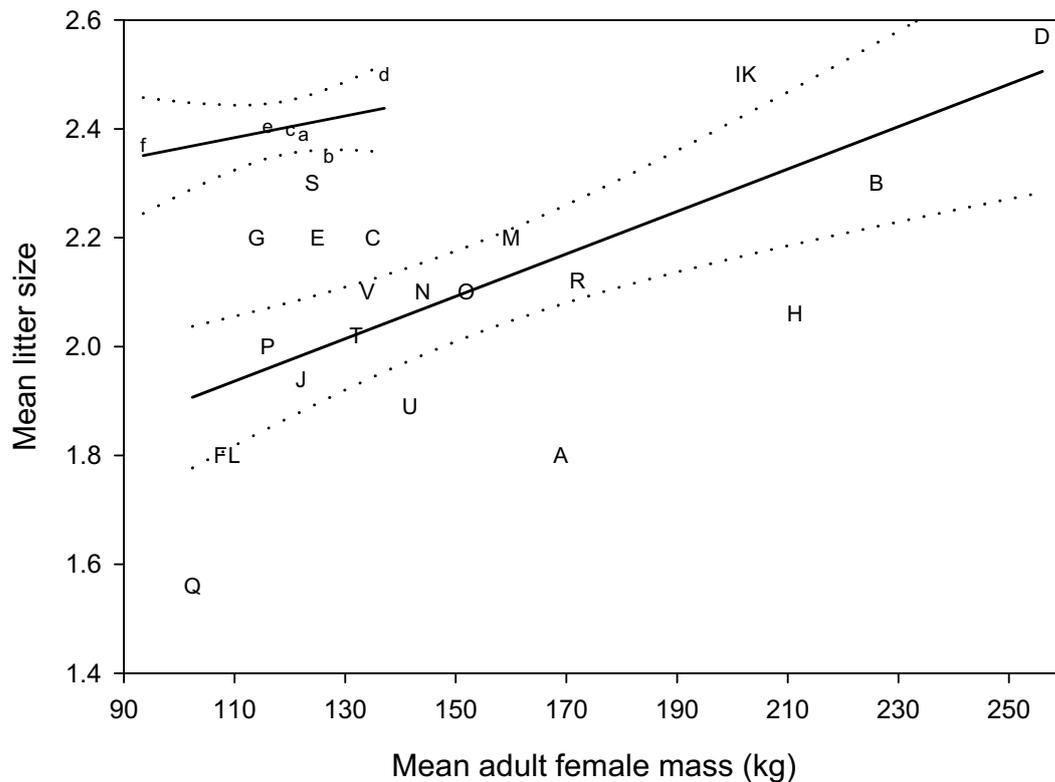
Table 1 Data used to analyze the relative degree of female reproductive investment in brown bear populations. Continent refers to the geographic location of the population (NA = North America, AS = Asia, EU = Europe); genetic lineage = mitochondrial DNA lineage[20,21]; persecution length (long: >500 years of human persecution; short: <150 years of human persecution by modern man); mean female mass = mean adult female brown bear body mass in kg; mean litter size = mean number of cubs per litter; black bear = presence (Yes) or absence (No) of sympatric black bear populations; symbol = symbol this population is referred to in Fig. 1; source = citation.

Population	Continent	Genetic lineage	Persecution length	Mean female mass	Mean litter size	Black bear	Symbol	Source
Admiralty Island	NA	5	short	169	1.8	No	A	[35]
Alaska Peninsula	NA	2	short	226	2.3	No	B	[35]
Alaska Range	NA	2	short	135	2.2	No	C	[35]
Black Lake	NA	2	short	256	2.57	No	D	[22]
East Front Montana	NA	6	short	125	2.2	Yes	E	[35]
Eastern Brooks Range	NA	2	short	108	1.8	Yes	F	[35]
Flathead	NA	6	short	114	2.2	Yes	G	[35]
Katmai NP	NA	2	short	211	2.06	No	H	[22]
Kenai Peninsula	NA	2	short	202	2.5	Yes	I	[22,35]
Kluane NP	NA	3	short	122	1.94	Yes	J	[22]
Kodiak Island	NA	2	short	202	2.5	No	K	[35,35]
MacKenzie Mountains	NA	3	short	110	1.8	Yes	L	[35]
McNeil Sanctuary	NA	2	short	160	2.2	No	M	[35]
Nelchina	NA	2	short	144	2.1	Yes	N	[35]
North Central Alaska Range	NA	2	short	152	2.1	Yes	O	[22]
Northern Yukon	NA	3	short	116	2	No	P	[35]
Southern Hokkaido	AS	4	short	102	1.56	No	Q	[36]
Susitna Valley	NA	2	short	172	2.12	Yes	R	[22]
Tuktoyaktuk	NA	3	short	124	2.3	No	S	[35]
Western Brooks Range	NA	2	short	132	2.02	No	T	[35]
Yakutia	AS	2	short	142	1.89	No	U	[22]
Yellowstone	NA	6	short	134	2.1	Yes	V	[a,37]
Dinara	EU	2	long	123	2.39	No	a	[29,38]
Leningrad Oblast	EU	2	long	127	2.35	No	b	[39]
Northern Sweden	EU	2	long	120	2.4	No	c	[31]
Southern Finland	EU	2	long	137	2.5	No	d	[40,41]
Southern Sweden	EU	1	long	117	2.4	No	e	[31]
Western Cantabria	EU	1	long	94	2.37	No	f	[42,43]

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