BEHAVIORAL ECOLOGY - ORIGINAL PAPER

The effects of primiparity on reproductive performance in the brown bear

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Abstract We studied the effects of primiparity on litter size, offspring size, and cub loss in brown bears (*Ursus arctos*) in two study areas (north, south) in Sweden from 1987 to 2006. Sexually selected infanticide (SSI) has been suggested previously as a mortality factor in our study populations. Females in the south became primiparous earlier than females in the north. Primiparous females had significantly smaller litters of cubs than multiparous females. We found no evidence that primiparity was costly in terms of the interlitter interval. Primiparous mothers had a higher probability of cub loss than multiparous mothers. The probability of cub loss was analyzed separately for the pre-mating and the mating season. The probability of cub loss by primiparous females in the pre-mating season increased with both increasing population density and deteriorating food conditions, whereas the probability of cub loss during the mating season decreased with increasing age of primiparity and increased with male turnover (a variable predicting SSI). The temporal patterns of cub loss by primiparous females suggested that the critical times for reproductive success by primiparous females were the pre-mating season (from birth to shortly after leaving the den) and the mating season. Cub loss in these periods was independent and caused by different factors. Cub loss before the mating season seemed to be most influenced by food conditions, whereas that during the mating season appeared to be caused by SSI.

Keywords Litter size · Litter survival · Sexually selected infanticide · Primiparity · *Ursus arctos*

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Introduction

Primiparity, or 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 females that have given birth more than once (multiparity) (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; Tuomi et al. 1983) are life history concepts that provide a theoretical basis for the relatively low performance of first-time breeders (Künkele 2000). In addition, primiparous females may not have reached maximum skeletal size, as would multiparous females (Schwartz et al. 2003b; Zedrosser et al. 2006). Larger females often produce larger and heavier offspring (Clutton-Brock 1988; Wauters et al. 1993), and larger offspring may have higher survival (Dahle et al. 2006).

Young females may have to make a relatively greater reproductive effort than fully grown females (Clutton-Brock 1991). Consequently, young females should be more likely to show evidence of reproductive costs (Festa-Bianchet and Côté 2008). Inexperience may also cause primiparous females to be energetically less efficient in offspring

production than multiparous females (Künkele 2000), and 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 infanticidal conspecifics, i.e., sexually selected infanticide (SSI) (Hrdy 1979).

We used long-term data (20 years) collected in two Scandinavian brown bear (*Ursus arctos*) populations to study reproductive performance and fitness consequences of first reproduction in a solitary mammalian carnivore exhibiting evidence of SSI. The brown bear is a typical capital breeder, and the earliest recorded age of primiparity is 3 years (Zedrosser et al. 2004). Litter size is variable, ranging from one to four cubs per litter (McLellan 1994) and there is evidence that young and old females produce fewer cubs per litter than prime-age adults (Craighead et al. 1995). Offspring stay with their mother for at least 1.5 years (Dahle and Swenson 2003a). Yearling offspring size in brown bears is positively related to food conditions and maternal size and negatively related to litter size and population density (Dahle et al. 2006). Several factors have been proposed as important for survival of brown bear cubs, including nutritional, social and disturbance factors (McLellan 2005; Miller et al. 2003; Swenson et al. 1997, 2001a, b); however, Swenson et al. (1997, 2001b) have suggested that SSI, a social factor, is the major agent of brown bear cub mortality in parts of Scandinavia, where 85% of all cubs disappeared during the mating season (Swenson 2003). Females use behavioral strategies that are interpreted as reducing the possibility of infanticide, such as spatial avoidance of adult males (Ben David et al. 2004; Wielgus and Bunnell 1994) or multi-male mating (Bellemain et al. 2006b).

We studied the reproductive performance of primiparous female brown bears by investigating if: (1a) the litter size of a primiparous mother is smaller than that of multiparous mothers, and (1b) the average body size of their yearlings is smaller than that of multiparous mothers' yearlings. We predicted that: (2) primiparous females would have a higher cost of reproduction, i.e., a longer interlitter interval, than multiparous females. We also predicted that: (3a) primiparous mothers would have a higher cub loss than multiparous mothers. For primiparous mothers, we predicted that cub loss: (3b) in the pre-mating season is positively related to population density, and negatively related to food conditions, female body size at primiparity, and age at primiparity; (3c) the probability of cub loss during the mating season is positively correlated to population density and male turnover, a variable predicting SSI (Swenson et al. 1997, 2001a, b; see "Materials and methods"), and negatively correlated to female body size at primiparity and age at primiparity.

Materials and methods

Study areas, study populations and field methods

The study was conducted in two areas in Scandinavia, 600 km apart. The southern study area, hereafter "the south", was in Dalarna and Gävleborg counties in south-central Sweden (61°N, 18°E). The rolling landscape is covered with coniferous forest, dominated by Scots pine, *Pinus sylvestris*, or Norway spruce, *Picea abies*, and contains a hunted bear population. The northern area, hereafter "the north", was in Norrbotten County in northern Sweden (67°N, 18°E). It is mountainous, with altitudes up to 2,000 m and a subalpine forest dominated by birch, *Betula pubescens*, and willows, *Salix* spp. and a coniferous forest of Scots pine and Norway spruce below the subalpine forest; see Zedrosser et al. (2006) for further details.

The study populations differed in some demographic parameters (Sæther et al. 1998), due in part to male-biased juvenile dispersal (Støen et al. 2006a, Sæther et al. 1998) and low rates of male immigration in the north (Swenson 2003; Swenson et al. 2001b). Illegal killing in the spring reduced the number of adult males in the north (Swenson et al. 2001b; Zedrosser et al. 2007a) and numbers remained stable but low during most of the study. In the south, adult males were more abundant and killed by legal hunting in the autumn (Swenson et al. 2001b; Zedrosser et al. 2007a). Cub survival was significantly lower in the south, perhaps due mainly to SSI (Swenson et al. 1997, 2001b). The study populations belong to different mitochondrial DNA lineages, but there is male-mediated genetic interchange between these lineages (Taberlet et al. 1995).

Bears were immobilized from a helicopter in mid-April in the south and early May in the north, shortly after den emergence (Zedrosser et al. 2007b). Head circumference (at the widest part of the zygomatic arch between eyes and ears) was measured with a tape measure and used as an index of individual size. Head circumference was used because Derocher and Stirling (1998) suggested that head measurements are more useful measures to compare populations of polar bears (*Ursus maritimus)* than body length. To avoid disturbing mothers with young cubs, almost no females were captured when they had cubs. To estimate head circumference at primiparity, we used study-area specific growth curves (Zedrosser et al. 2006).

We only used female brown bears of known age (i.e., captured as yearlings with their radio-collared mother). We counted cubs with radio-collared mothers from the air or the ground 3 times annually; just after leaving the natal den, at the end of the mating season, and just prior to entering the den in the fall (September) or when capturing the female and her yearlings in April/May the following year. If counts of cubs were uncertain, due to poor

visibility, counts were conducted on another day until the number of cubs was certain. We assumed that cubs had been lost in the den or shortly after leaving it when a lactating female was captured without cubs. We defined the pre-mating season from when a bear left the den (usually middle to late April in the south, beginning of May in the north) until the second week of May, and the mating season the third week of May until the first week of July (Dahle and Swenson 2003b).

Food condition index

We used spring body mass of yearlings ($n = 347$, range of body mass: 8–45 kg) to construct an annual index of the food conditions for each study population the year before. We controlled for the variables that influence yearling mass independently of food conditions (Dahle et al. 2006). The standardized residuals from this regression for each year and area were used as the food condition index for the year when the yearlings had been cubs (Zedrosser et al. 2006).

Individual population density index

The population density around each individual (within a radius of 17.84 km, corresponding to bears per 1,000 km^2) was estimated in both study areas, based on the high proportion of radio-collared bears and documented population growth rates [see Zedrosser et al. (2006) for a more detailed description]. In the south, the population size was estimated based on a DNA analysis of scats in 2001 and 2002 (Bellemain et al. 2005). The temporally-corrected individual density index for radio-collared individuals in our analysis was based on the location of these bears, that of individuals genetically identified by the scat sampling (71% of the radio-collared bears) was represented in the scat samples (Bellemain et al. 2005) and the population growth rate (Kindberg and Swenson 2006; Sæther et al. 1998). Because the density estimates were based on genetic analysis of scat samples, we were not able to identify age classes in this area. 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. 2001b). We used the locations of radio-collared bears, corrected to include subadult males, and growth rate of the population to calculate an individual density index as in the south (Zedrosser et al. 2006).

Male turnover

Since 1981, hunters who kill a brown bear in Sweden have been required to report the sex and kill location, body measurements, and to deliver a tooth for age determination and tissue samples to the authorities. To estimate the number of adult males killed within 40 km of a mother with cubs, we calculated the arithmetic center of the 95% minimum convex polygon (MCP) home range for every female with cubs and, for each year, determined the number of adult males that had died there 1.5 years previously. This included hunter-killed males, accidental deaths, damage-control kills, 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 are within this distance from the mothers (Bellemain et al. 2006b). 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 an adult as ≥3 years of age, because the first age of male reproduction is 3 years in both study areas (Bellemain et al. 2006b; Zedrosser et al. 2007a). The software package Ranges 6 (Anatrack, Wareham, Dorset, UK) was used for calculating home range centers.

Statistical analysis

Because several individuals had several litters, we used generalized linear mixed models (GLMM) to control for the effects of individual identity when evaluating differences in cub litter sizes between primiparous and multiparous females (Steel and Hogg 2003). The difference in yearling body size of primiparous and multiparous mothers was also analyzed with a GLMM. The response variable was head circumference (in centimeters) 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. (2006) to be important for yearling body size in these populations (i.e., maternal body size, litter size, sex of offspring, population density, cohort, study area). We analyzed whether there was a difference in probability of losing cubs for primiparous and multiparous females with a GLMM. We chose "loss of one or more cubs" (0 = no cub loss, 1 = cub loss) as the binary response variable, while controlling for the effects of study area. The factors determining cub loss for 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 to 2004: study area (south or north), male turnover (the number of adult male deaths within 40 km 1.5 years previously), age of primiparity (4–7 years), body size at primiparity, local population density, and food condition indices. Ages 6 and 7 were always pooled for sample size reasons. We selected the best model in a backward elimination procedure, choosing predictor variables 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. Due to differences in data availability, the sample sizes differed among tests and models. The statistical software R 2.7.2 (R Development Core Team, http://www.r-project.org) was used in all analyses.

Results

We obtained ages of primiparity for 59 females, 21 in the north and 38 in the south, during 1987–2006. Primiparous females in the south were significantly younger than those in the north (Table 1; two sample *t*-test, $t_{47.009} = 3.553$, $P < 0.001$). There was a trend towards a difference in the age of first successful litter between the study areas (north, 6.00 ± 1.29 years; south, 5.39 ± 0.74 years; two sample *t*-test, $t_{26.001} = 1.845$, $P = 0.075$). For 11 females in the south and three females in the north we were unable to determine the age of first successful litter (Table 1).

There was no significant difference in litter size of primiparous females in the south and in the north (Table 2; two sample *t*-test, $t_{32.134} = 1.416$, $P = 0.167$). Primiparous females had significantly smaller litters than multiparous females, when controlling for the effect of the study area (Table 2; GLMM, β status$_{primiparous/multiparous} = 0.381$, SE = 0.129, $df = 127$, $t = 2.954$, $P = 0.004$, $n = 211$, number of groups = 83; β status$_{primiparous/multiparous} \times$ study area = 0.153, $P = 0.565$; β study area = -0.204, $P = 0.121$). As Dahle et al. (2006) reported previously, yearlings of multiparous females were about 14% larger than yearlings of primiparous females, when controlling for other significant

factors found to be important for yearling body size in these populations (our GLMM, $\beta = 1.145$, SE = 0.519, $df = 231$, $t = 2.205$, $P = 0.028$, number of observations = 303, number of groups = 66).

There was no significant difference in the interlitter interval of primiparous and multiparous females in the south (Table 2; two sample *t*-test, $t_{36.584} = -1.581$, $P = 0.122$) or in the north (Table 2; two sample *t*-test, $t_{13.519} = 0.543$, $P = 0.596$). The interlitter interval of primiparous and multiparous females that had lost their entire litter did not differ significantly in the south (Table 2; two sample *t*-test, $t_{22.304} = 0.464$, $P = 0.648$); the sample sizes in the north were too low for a meaningful comparison (Table 2). Also, there was no significant difference in the litter intervals of primiparous and multiparous females that experienced only partial or no loss of a litter in the south (Table 2; two sample *t*-test, $t_{9.7} = 1.052$, $P = 0.318$) and in the north (Table 2; two sample *t*-test, $t_{9.208} = 0.822$, $P = 0.432$). A binary model showed that, when controlling for the effect of study area, primiparous females had a significantly higher probability of losing one or more cubs than multiparous females (GLMM, $\beta = -0.840$, SE = 0.320, $df = 179$, $t = -2.625$, estimated odds ratio = 0.432, $P = 0.009$; number of observations, 270; number of groups, 90).

The proportion of primiparous mothers that lost cubs varied with age of primiparity and between study areas (Table 3). In the south, cub loss by primiparous females occurred evenly before and during the mating season, but in the north mostly during the mating season (Table 3). No primiparous females in our sample were observed to lose cubs after the mating season (Table 3).

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 1987–2006

Study area	Mean age of primiparity ($\pm$ SE)	4 Years	5 Years	6 Years	7 Years	*n*
South	4.71 ± 0.65[a]	0.39	0.50	0.11	0	38
North	5.29 ± 0.56[b]	0	0.76	0.19	0.05	21

[a] Three females of potentially reproductive age disappeared (known death, loss of radio-collar) before reproducing (two at 4 years of age, one at 5 years of age)

[b] Eleven females of potentially reproductive age disappeared (known or suspected death, loss of radio-collar) from the population before reproducing (nine at age 5 years, one at age 6 years, one at age 7 years)

Table 2 Reproductive parameters of primiparous and multiparous female brown bears in two study areas in Scandinavia, 1987–2006

Parameter	Primiparous		Multiparous	
	South	North	South	North
Litter size	1.92 ± 0.61 (27)	2.22 ± 0.73 (18)	2.38 ± 0.83 (109)	2.49 ± 0.78 (57)
Litter interval, overall	1.58 ± 0.71 (26)	2.58 ± 1.08 (12)	1.78 ± 0.64 (100)	2.40 ± 0.71 (47)
Litter interval, after loss of entire litter	1.06 ± 0.25 (16)	1.5 ± 0.71 (2)	1.03 ± 0.17 (33)	1.5 ± 0.53 (8)
Litter interval, after no/partial loss of litter	2.33 ± 0.5 (9)	2.88 ± 1.05 (9)	2.15 ± 0.44 (67)	2.58 ± 0.59 (39)

Values of parameters are shown as mean $\pm$ SE (sample size). The litter intervals are given in years

Table 3 Timing of cub loss in relation to age at primiparity for primiparous female brown bears in two study areas in Scandinavia in 1987–2006

Study area	Age at primiparity	Timing of cub loss			No loss	n
		Pre-mating season[a]	Mating season[b]	Post-mating season[c]		
South	4	6 (0.50)[d]	7 (0.58)[d]	–	1 (0.08)	12[d]
	5	4 (0.27)	6 (0.40)	–	5 (0.33)	15
	6	–	1 (0.25)	–	3 (0.75)	4
North	5	1 (0.08)	2 (0.15)	–	10 (0.77)	13
	6		1 (0.33)	–	2 (0.67)	3
	7	–	1 (1)	–		1

[a] Pre-mating season is the time period from leaving the den until the second week of May. The proportion is given *in parentheses*

[b] Mating season is the time period from the third week of May until the first week of July. The proportion is given *in parentheses*

[c] Post-mating season is from the second week of July until hibernation. The proportion is given *in parentheses*

[d] Two females lost the first cub during the pre-mating season and the second cub during the mating season; these bears are counted in each column but only once in n

The binary model examining the probability of losing one or more cubs by primiparous mothers before the mating season showed that the probability of cub loss increased significantly with population density and decreased significantly with improving food conditions (Table 4; model a). The other variables and interactions tested were not significant and were removed in this order: body size × study area, $\beta < 0.001$, $P = 0.999$; food conditions × study area, $\beta = -0.001$, $P = 0.999$; population density × study area, $\beta = -0.003$, $P = 0.997$; population density × food conditions, $\beta = -0.313$, $P = 0.819$; study area, $\beta = 0.567$, $P = 0.773$; body size × food conditions, $\beta = -10.897$; $P = 0.409$; body size × population density, $\beta = 2.551$,

Table 4 Model a, the probability that a primiparous female brown bear lost at least on dependent offspring before the mating season ($n = 31$); and model b, the probability that a primiparous female brown bear lost at least one dependent offspring during the mating season ($n = 38$) in two study areas in Scandinavia from 1987–2006

Variable	β	SE	z	OR	P
Model a loss before mating season					
Sqrt (population density)	0.736	0.309	2.381	2.088	0.012
Food conditions	−1.581	0.847	−1.866	0.206	0.062
Model b loss during mating season					
Age at primiparity					
4	0	0	0		0
5	−3.320	1.448	−2.293	0.036	0.022
6 + 7	−1.751	1.396	−1.254	0.174	0.210
Male turnover	2.467	1.136	2.171	11.787	0.030

The binary response variable in both models was the probability of "loss of one or more cubs". The predictor variables available in both models 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 (ages 6 and 7 are pooled for sample size reasons), body size at primiparity, and food conditions, while controlling for population density. β Estimated coefficient, *OR* estimated odds ratio

$P = 0.416$; body size × food conditions, $\beta = -12.225$, $P = 0.385$; body size, $\beta = 9.248$, $P = 0.186$; age, factor age 5 years, $\beta = -1.852$, $P = 0.1738$, factor age 6 years, $\beta = -20.421$, $P = 0.994$.

A binary model examining the probability of losing one or more cubs by primiparous mothers during the mating season showed that the probability of cub loss decreased with age (although significant only at age 5 in relation to age 4) and was significantly and positively influenced by the number of males dying within 40 km 1.5 years previously (male turnover) (Table 4; model b). The other variables and interactions tested were not significant and were removed in this order: population density × food conditions, $\beta = -0.391$, $P = 0.672$; population density × study area, $\beta = -0.995$, $P = 0.592$; body size × population density, $\beta = 3.931$, $P = 0.358$; body size × study area, $\beta = -10.131$, $P = 0.267$; body size × food conditions, $\beta = 7.757$, $P = 0.167$; body size, $\beta = 0.201$, $P = 3.638$, $P = 0.956$; study area × male turnover, $\beta = 4.393$, $P = 0.116$; population density, $\beta = 0.297$, $P = 0.325$; food conditions × study area, $\beta = 1.823$, $P = 0.270$; study area, $\beta = 0.319$, $P = 0.717$; food conditions, $\beta = -0.391$, $P = 0.518$.

Discussion

As predicted, primiparous females had fewer cubs and smaller yearlings than multiparous females. There may be a general bias in our data towards larger yearlings, as we only measured individuals surviving their first year; cubs that died in their first year of life may have been smaller on average than those that survived. Contrary to our predictions, we did not find evidence that primiparity was costly in terms of the interlitter interval, but in accordance with our predictions primiparous mothers had a higher probability

of cub loss than multiparous mothers. The probability of cub loss by primiparous females in the pre-mating season increased with both increasing population density and deteriorating food conditions, whereas the probability of cub loss during the mating season decreased with increasing age of primiparity and increased with male turnover. Cub loss by primiparous females after the mating season did not seem to be important in our study populations. This suggests that the critical times for reproductive success by primiparous females are the periods from birth to shortly after leaving the den and the mating season, and that cub loss in these periods is independent.

Patterns of lowered reproductive success by young and primiparious reproducers have been observed in birds (e.g., Curio 1983; Lack 1966; Ollason and Dunnett 1988) and mammals (e.g., Clutton-Brock 1991; Clutton-Brock et al. 1988; Festa-Bianchet et al. 1995; Hellgren et al. 1995), including ursids (Craighead et al. 1995; Derocher and Stirling 1994; Schwartz et al. 2003a). The causes for this lowered performance of primiparous individuals may include physical maturation, lower reproductive experience, and changes in dominance rank (Clutton-Brock 1988).

The exclusion of primiparous female brown bears by more dominant individuals from habitats with a high availability of protein, such as salmon (*Oncorhynchus* spp.), has been reported from North America (Ben David et al. 2004), and may result in lowered reproductive performance. However, salmon is not a food source for bears in Sweden (Dahle et al. 1998; Persson et al. 2001; Swenson et al. 1999) and other major food items (i.e., berries, ants) are more evenly distributed over the landscape. Female brown bears reach 90% of their asymptotic body size at approximately 4–5 years of age in Scandinavia (Zedrosser et al. 2006), but in North American inland populations (i.e., no or little access to spawning salmon) females can continue to grow until 9 years of age (Kingsley et al. 1988). The smaller litters in primiparous brown bears may therefore be caused by age-related changes in the allocation of energy to growth and reproduction. This trade off also involves offspring body size, because body size and mass of yearling brown bears are positively related to maternal size (Dahle et al. 2006).

Primiparous females in the south were significantly younger than those in the north. Zedrosser et al. (2006) found that 4-year-old females in the north were somewhat smaller than in the south, perhaps due to less favorable climatic conditions in the north, which may prevent 4-year-old females from reproducing. In addition, Støen et al. (2006b) found evidence for reproductive suppression in the south, because the mean age of primiparity was 4.3 years for dispersing females and 5.2 years for philopatric females. Although 32% of subadult females disperse in the north and 46% in the south (Støen et al. 2006a), dispersing females in the north do not seem to be able to use the opportunity to reproduce 1 year earlier.

Because primiparous female brown bears are often smaller than multiparous females (Zedrosser et al. 2006), there could be fitness costs of primiparity, which has been suggested for other mammals (e.g., Festa-Bianchet and Côté 2008; Green and Rothstein 1991). If bears incur such costs, primiparous females may be less likely to reproduce the year after successfully weaning their cubs, i.e., their interlitter intervals should be longer than for multiparous females. We found no difference in the interlitter interval of primiparous and multiparous females, suggesting that primiparous females do not incur short-term reproductive costs great enough to increase the interval to their second litter. Due to low sample sizes, we were not able to test whether the youngest primiparous females (i.e., age 4 years) had a longer interlitter interval than older primiparous females. Primiparity also did not entail future fitness costs in terms of survival, as no primiparous females in our sample with known causes of mortality died of natural causes after weaning their young.

Primiparous mothers had a higher probability of losing cubs than multiparous mothers. Several factors have been proposed as important for bear cub survival (McLellan 2005; Miller et al. 2003; Swenson et al. 1997, 2001b). Our results suggest that different mortality factors may be important during different times of the year. Cub loss by primiparous females before the mating season was related to population density and the food conditions the previous year. Access to food may be especially problematic for a young female in years with less favorable food conditions, especially when population density is high. Several primiparous females were captured shortly after leaving the den with either milk in the nipples or nipples that showed signs of being used by cubs. This suggests that those females gave birth, but their cubs died before den abandonment. We only rarely found dead cubs; they may have been eaten by the mother. These females may have given birth instead of aborting the pregnancy when they were in poor condition following a poor food year, as bear cubs are small relative to their mothers (Oftedal and Gittleman 1989) and thus relatively cheap to produce.

The probability of cub loss by primiparous females during the mating season was positively related to male turnover, suggesting that SSI may be a mortality factor for cubs of primiparous females. The death of adult males may promote the influx of immigrating males and/or possibly realignment of the home ranges of adult males (McLellan 2005; Swenson 2003), resulting in males coming into contact with litters that they did not father. A correlation between male turnover and cub mortality has been reported earlier from this study area (Swenson et al. 1997, 2001b). Our results also show that primiparous mothers, especially

those 4 years of age, lose more cubs than multiparous females. First-time breeders may lack refined behavioral skills associated with foraging and parental care (Becker et al. 1998; Wang and Novak 1994). Primiparous mothers may be less efficient in defending their cubs against infanticidal males, have less knowledge of local dominance hierarchies, and less experience in avoiding potentially infanticidal individuals.

The importance of SSI in brown bear populations remains under debate (e.g., McLellan 2005; Miller et al. 2003; Swenson et al. 1997, 2001b; Wielgus and Bunnell 2000). Researchers in Scandinavia have found support for the SSI hypothesis (Bellemain et al. 2006a; Swenson et al. 1997, 2001b), whereas results from North America are not as clear (Ben David et al. 2004; McLellan 2005; Miller et al. 2003; Wielgus and Bunnell 2000). One possible explanation for some of these differences may be the higher age of primiparity in North America, because our results suggest that females that become primiparous at older ages lose fewer cubs during the mating season.

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