

# Socially induced delayed primiparity in brown bears *Ursus arctos*

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Received: 1 December 2005 / Revised: 16 May 2006 / Accepted: 23 May 2006 / Published online: 29 June 2006  
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**Abstract** 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 (*Ursus arctos*) 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 the 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 ( $n=8$ ) and 5.2 years in

philopatric females ( $n=10$ ). Only the overlap with the mother's home range, and not body size, body mass, growth, local population density, or overlap with the 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.

**Keywords** 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 of finding suitable offspring-rearing space, familiarity with the local area and neighbors 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 behavioral 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

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Communicated by M. Festa-Bianchet

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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 intersexually 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 (*Oncorhynchus* spp.) spawning streams (see Interagency Grizzly Bear Committee 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 matrilinear 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.

## Materials and 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 (61° N, 18° 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 seven 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 the 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, 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 2 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  $58 \pm 13$  (mean  $\pm$  SD, range of 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 old 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 toward 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  $121 \pm 50$  (mean  $\pm$  SD, range of 26–185). The corresponding annual number of locations of these mothers' philopatric daughters for these years ( $n=42$ ) was  $31 \pm 10$  (range of 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  $61 \pm 42$  (range of 26–144). The corresponding annual number of locations of their daughters after natal dispersal for these years ( $n=16$ ) was  $31 \pm 10$  (range of 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 old 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  $96 \pm 43$  (range of 22–184). The corresponding annual number of locations of these fathers' daughters for these years ( $n=38$ ) was  $29 \pm 11$  (range of 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. Immobilized 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, which was based on tracks and markings from the young 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 the eyes and ears) was measured with a tape and used as a measure of the overall body size of an individual (Zedrosser et al. 2006). 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 centimeters 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 noninvasive sampling of scats, was carried out in the study area 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 of the center of the focal bear's home range (which corresponds to the

density of bears per 1,000 km<sup>2</sup>), based on the centers of the locations of all scat samples for each individual (Zedrosser et al. 2006). 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 noninvasive population sampling, we divided the individual density index by 0.71 (Zedrosser et al. 2006). 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 et al. 2006). 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  $I_d$  for an individual bear in year  $\gamma$  (for  $\gamma < 1993$ ) was then  $tI_d = I_d / 1.16^{(1993-\gamma)}$ , where  $I_d$  is the index for 2001–2002 (see Zedrosser et al. 2006 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, while 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  $2.25 \pm 0.89$  (mean  $\pm$  SD, range of 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 seven 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  $4.8 \pm 0.7$  years, and as 4-year-olds, their average head circumference was  $56.0 \pm 2.2$  cm, body mass was  $77.9 \pm 10.4$  kg, and the average individual population density index was  $31.6 \pm 18.4$  bears/1,000 km<sup>2</sup>. The 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 the bears were 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 seven (87.5%) of the nine daughters that gave birth as 4-year-olds had dispersed, measuring head circumference and body mass approximately 4 months after parturition could bias our data toward 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 the age of primiparity (Table 2).

Growth rate and nourishment as young affect primiparity in several species (Reiter and LeBoeuf 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 ( $31.8 \pm 16.3$ ) and the area where the daughters ( $n = 18$ ) gave birth to their first litter ( $31.8 \pm 19.5$ ,  $t = 0.002$ ,  $p = 0.999$ ). This was true both for philopatric daughters where the population density index was  $32.4 \pm 15.3$  in the natal area and  $37.2 \pm 22.5$  in the area where they gave birth to their first litter ( $n = 10$ ,  $t = 1.206$ ,  $p = 0.258$ ) and for dispersing daughters where the population density index was  $31.0 \pm 18.5$  in the natal area and  $24.9 \pm 13.4$  in the area where they gave birth to their first litter,

**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			$t^a$	$p$
	$X$	SD	$n$	$X$	SD	$n$		
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/1,000 km <sup>2</sup> )								
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

<sup>a</sup>Two-sample  $t$  test

( $n=8$ ,  $t=1.208$ ,  $p=0.266$ ). Some daughters had their first litter when they were 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 ( $39.0\pm 20.8$ , used in the GLM model) and the area where they had their first litter ( $39.2\pm 22.8$ ,  $t=0.083$ ,  $p=0.94$ ).

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 six daughters were located within their fathers' 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 they were 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, nongregarious, wild carnivore. Dalerum et al. (2006) 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. 2006).

The reasons for reproductive suppression in brown bears, similarly to many gregarious species, could include inbreeding avoidance (Wolff 1992) or minimization of 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 fathers' home range and those that overlapped with their fathers until primiparity; however, due to the low sample size in our study, we cannot rule out the importance of the father's influence. Because of the low risk of inbreeding shown by theoretical modeling (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 the frequent occurrence of multipaternal litters (Bellemain et al. 2005), indicate the frequent exposure of young females to unrelated males. Frequent exposure of young females to unrelated males may

**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 bears were 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	$\beta$	SE	$df$	$t$	$p$
3 years old					
Density (bears/1,000 km <sup>2</sup> )	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 (bears/1,000 km <sup>2</sup> )	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

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. 2006), 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; Bunnell and Tait 1981) and in 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 the age of primiparity in our GLM models. The reason might be because small Scandinavian brown bear females show compensatory growth (Zedrosser

et al. 2006), 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 growth rate had 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 the age of primiparity in several mammalian species (Festa-Bianchet et al. 1995, 1998; Forchhammer et al. 2001; Bonenfant et al. 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 the 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 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.

**Acknowledgements** This study was funded by the Norwegian Directorate for Nature Management, the Swedish Environmental Protection Agency, the Swedish Association for Hunting and Wildlife Management, World Wildlife Fund Sweden, the Research Council of

Norway, and the Norwegian University of Life Sciences. Andreas Zedrosser was financially supported by the Austrian Science Fund Project P16236-B06. We thank the personnel in the Scandinavian Brown Bear Research Project for their assistance in the field and Orsa Communal Forest for field support. We thank Ali Nawaz and Bjørn Dahle for comments on an earlier draft and Solve Sæbø for statistical help. All capture and handling of bears reported in this paper complied with the contemporary laws regulating the treatment of animals in Sweden and Norway and was approved by the appropriate management agencies and ethical committees in both countries.

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