

DISTANCE-DEPENDENT EFFECT OF THE NEAREST NEIGHBOR: SPATIOTEMPORAL PATTERNS IN BROWN BEAR REPRODUCTION

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Abstract. In mammals, reproductive synchrony and reproductive suppression usually are found in social, group-living species, which often display hierarchical relationships among related animals. Some individuals, particularly younger, philopatric females beyond the age of sexual maturity, may not raise offspring because they are suppressed by other individuals. Although brown bears (*Ursus arctos*) are a solitary species, the existence of socially induced delayed primiparity of philopatric females has been documented. Here we show further evidence for interactions of a population-regulatory nature that are typically associated with social species. We found that an adult female's probability of having cubs in a given year was influenced by whether or not her nearest neighboring adult female had cubs. At short distances (≤ 10 km) between the home range centroids of neighboring females, females with cubs had a negative effect on their neighboring female's probability of having cubs of the year. At distances > 10 km and ≤ 20 km, the effect reversed, and it disappeared beyond 20 km. We argue that reproductive suppression is probably caused by resource competition among females living close to each other. Previously, similar population regulation mechanisms have been found only in group-living mammals. Thus, social interactions and behavior in solitary carnivores may be more flexible than usually assumed.

Key words: brown bears; females; population regulation; reproductive competition; reproductive suppression; reproductive synchrony; Scandinavia; sexually selected infanticide; sociality; *Ursus arctos*.

INTRODUCTION

Reproductive synchrony refers to several females giving birth within a few days or weeks, i.e., parturition is temporally clustered (Ims 1990). In mammals, it has been usually described for social, group-living species, from rodents to ungulates and large carnivores (e.g., Rutberg 1984, Johannesen et al. 2000, Packer et al. 2001, Gilchrist 2006). Also, group-living and cooperatively breeding mammals often display hierarchical relationships among related animals, in some cases manifested by reproductive suppression (Creel and Macdonald 1995, Moelhman and Hofer 1997). This generally affects young, philopatric females through behavioral or physiological mechanisms (Wasser and Barash 1983, Brant et al. 1998, Hackländer et al. 2003).

There are several possible causes of spatiotemporal patterns in reproduction (Ims 1990). Environmental factors, like food availability, can play an important role in synchronizing reproduction (Hudson and Cattadori 1999), but also internal factors, like biological clocks

and social signals exchanged among female individuals within a population, may synchronize reproduction in birds and mammals (Ims 1990). In addition, the existence of male-induced reproductive synchrony has been observed in lions (*Panthera leo*), with the turnover of males causing birth synchrony within the pride following infanticidal killing by males (Packer and Pusey 1983).

However, some factors facilitate reproductive asynchrony rather than synchrony. Competition for breeding among females can explain why older females suppress reproduction in younger ones to reduce competition for limited resources, which has been shown for different mammal groups, such as rodents (Eccard et al. 2002, Hodges et al. 2002, Wolff et al. 2002), carnivores (e.g., Moelhman and Hofer 1997), and primates (e.g., Digby 1995). Female reproductive suppression, likely instigated by adult females, was suggested to explain delayed primiparity in brown bears (Støen et al. 2006b), which could be in accordance with the reproductive-competition hypothesis (e.g., Wolff et al. 2001, 2002). Sexual selection also may favor reproductive asynchrony in species where paternal investment in young is unimportant (Ims 1990). Reproductive asynchrony can increase the opportunity for optimal male choice because each

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receptive female can attract more males when no other receptive females are present, and, if space and other resources are limiting, it can be advantageous for females with size-oscillating territories to reproduce out of synchrony with their neighboring territory holders (e.g., Ims 1990).

In this study we investigated whether there are spatiotemporal reproductive patterns in brown bears (*Ursus arctos*), i.e., if reproductive females living near each other influenced each other's reproduction. Brown bears exhibit two-, three-, and four-year reproductive cycles, but can give birth every year if the cubs of the year are lost. A number of different factors may favor either reproductive synchrony or asynchrony in Scandinavian brown bears. Environmental factors, such as between-year differences in food availability, could promote reproductive synchrony among neighboring females, i.e., most females giving birth in years with favorable food conditions. In some populations of North American black bears (*Ursus americanus*) reproduction is controlled mainly in a density-independent way by nutritional factors that fluctuate in abundance from year to year (Rogers 1976, 1987, Bunnell and Tait 1981, Beecham 1983, Eiler et al. 1989, Pelton 1989, McLaughlin et al. 1994). Sexually selected infanticide by males (Hrady 1979), a major reason for bear cub mortality in parts of Scandinavia (Swenson et al. 1997, 2001), also could promote reproductive synchrony, because infanticide shortens the time to the mother's next estrus (Swenson et al. 1997, Bellemain et al. 2006a), and affects several females simultaneously within the home range of a perpetrating male.

Dominance behavior during the mating season, leading to female reproductive suppression, might cause reproductive asynchrony in brown bears. We have already found evidence for female–female competition and dominance behavior in Scandinavian brown bears, where related females are spatially structured into matrilineal assemblages (Støen et al. 2005): (1) natal dispersal is inversely density dependent (Støen et al. 2006a), (2) there is a delayed primiparity of philopatric females, probably driven by resource competition within female hierarchies that causes reproductive suppression in young females (Støen et al. 2006b), (3) competition among female siblings forces the smaller one to disperse (Zedrosser et al. 2007), (4) unrelated females are excluded from matrilineal assemblages (Støen et al. 2005), and (5) home range size of both adult and subadult females are inversely related to density (Dahle and Swenson 2003c, Dahle et al. 2006). Also, Beckmann and Berger (2003) found that black bears were distributed primarily in an ideal-despotic manner in their study sites. Moreover, the lack of paternal care in brown bears, and the females' oscillating home range during their multiyear reproductive cycle (Haroldson et al. 2002, Dahle and Swenson 2003b) may promote reproductive asynchrony rather than synchrony (Ims 1990). Brown bear females roam to mate and mate with

several males (Dahle and Swenson 2003b, Bellemain et al. 2006b), so a lower number of females available to males in the breeding season, which would be facilitated by reproductive asynchrony, may increase mating possibilities for the females in estrus.

MATERIAL AND METHODS

Study species and study areas

The brown bear is a large carnivore with a promiscuous mating system (Pasitschniak-Arts 1993, Schwartz et al. 2003, Bellemain et al. 2006b). The mating season lasts from late May to early July (Dahle and Swenson 2003b). Implantation of the embryos is delayed (e.g., Spady et al. 2007), and female bears give birth to 1–4 offspring while hibernating in dens during winter (Pasitschniak-Arts 1993). Offspring separate from their mothers when they are 1.4–3.5 years old (McLellan 1994). In Sweden, females reproduce every two to three years (Dahle and Swenson 2003d). In south-central Sweden, 95% of the litters are weaned as yearlings (Dahle and Swenson 2003a), whereas only 53% of the litters are weaned as yearlings in northern Sweden (Dahle and Swenson 2003d). Females usually separate from their offspring during the mating season prior to mating (Dahle and Swenson 2003b; see Plate 1). In Scandinavia young females reach sexual maturity at the age of 3–5 years (Swenson et al. 1995), whereas they are usually older in North American populations (McLellan 1994, Hilderbrand et al. 1999).

Brown bears are solitary, but hierarchies develop, for instance, when they aggregate at food sources (Craighead et al. 1995, Gende and Quinn 2004). They are usually not considered to be territorial (Pasitschniak-Arts 1993, Schwartz et al. 2003), but natal dispersal and home-range size have been shown to be inversely density dependent, suggesting some form of territorial behavior in brown bears (Dahle and Swenson 2003c, Dahle et al. 2006, Støen et al. 2006a).

Our data came from two study areas. The southern study area is situated in Dalarna and Gävleborg counties, south-central Sweden, and Hedmark County, southeastern Norway (61° N, 18° E) and covers the southern part of the southernmost brown bear subpopulation in Scandinavia. Elevations range from ~200 m in the southeast to about ~1000 m in the west. Most of the area is below the timberline, which is at ~750 m. Lakes and bogs are common, but most of the hilly landscape is covered with intensively managed coniferous forest, dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). The northern study area is situated in Norrbotten County in Sweden (67° N, 18° E). The area is rolling, with elevations <300 m in the east, but is dominated by mountains that rise to >2000 m in the west. Northern boreal coniferous forest dominates, but there are extensive subalpine birch (*Betula pubescens*) forests. Detailed descriptions of the study areas can be found in Dahle and Swenson (2003d) and Zedrosser et al. (2006). For capture and marking

procedures, see Arnemo et al. (2006) and Arnemo and Fahlman (2007).

We analyzed data from 76 radio-marked females ≥ 4 years old (20 from the north, 56 from the south) during the period 1987–2006. Most of the bears were captured in spring, after den emergence, when yearlings were with their known, previously radio-collared mother; and/or the mother was known through genetic analyses (Bellemain et al. 2006b). The bears were located weekly or biweekly during their active period using standard triangulation methods from the ground or the air (Dahle and Swenson 2003a). The females were systematically observed from helicopters in spring to determine whether they had cubs, that is, to know if they gave birth that year. If not accompanied by cubs, the females were captured in spring and examined for lactation to determine if they had suckled cubs. In addition, we visited dens in the southern study area to determine whether young had been present outside the den, which was based on tracks and markings from the young climbing in nearby trees. In the northern study area, virtually 100% of the adult bears were radio-marked. Up to 80% of the adult females and 50% of the adult males (Swenson et al. 2001, Solberg et al. 2006) were radio-marked and relatively evenly distributed in the southern study area, with some variation during the 20-year study period.

Home-range centroid estimation for the annual active season

We used females with at least six relocations (range, 6–23; median, 16) to calculate annual home-range centroids, which were needed to determine neighbors, distance between them, and density. The distance between a focal female and its nearest neighbor in a given year was calculated as the straight-line distance between their annual home-range centroids. In the southern area, the mean date of den emergence was 20 April and that of entry was 28 October for radio-marked females (Friebe et al. 2001), whereas it was 10 May and 9 October, respectively, in the northern area (Manchi and Swenson 2005). Thus, we used only locations from May to September. To minimize autocorrelation, centroids were estimated using only the first position in a week if several positions were available for the same week. Female dyads were excluded from the analysis when this distance exceeded 40 km, because, even if the proportion of adult marked bears was very high, we did not know every breeding age female in the population. Thus, the probability that we knew the true nearest female decreased with increasing distance, as there was more space for unmarked females.

Statistical analysis

In order to test if reproductive females living near each other influenced each other's reproduction, we used logistic regression to evaluate the effect of the following variables on the probability of an adult female having cubs of the year in a given year: (1) age category of the

focal female (4–6, 7–12, >12 yr); (2) distance to the nearest known (radio-marked) neighboring adult female (≤ 10 km between home-range centroids, >10 and ≤ 20 km, >20 km up to 40 km); (3) the nearest neighboring adult female having cubs of the year or not (yes, no); (4) the nearest neighboring adult female was the focal females' mother (yes, no); (5) study area (north, south); and (6) environmental condition index. The spring body mass of yearlings in each year and study area was used to construct an index of the general food condition of the study populations for the previous year, while they were cubs (see Zedrosser et al. 2006).

Focal females had reproduced at least once before or during the first year of inclusion in the analysis. Our most general model included all of the above variables and meaningful two-way interactions among them. Among the ecological determinants of reproductive success, intraspecific competition and density-dependent effects have received much attention (e.g., Koskela et al. 1999). We evaluated the possible influence of density on the outcome of the analysis by using a local density index calculated for each year and study area, based on radiolocations of all collared bears, and local density using location of individual bears identified from DNA in scats collected by hunters during an intensive census (see Zedrosser et al. 2006 for a detailed description). Density (log-transformed) was inversely related to distance to the nearest neighbor ($F = 142.3$, $df = 1$, 427 , $P < 0.001$); thus, at a first stage we only included distance to the nearest neighbor in the model. To verify that possible effects of nearest neighbor distance were not solely an artifact of local density, we cut density into 20 narrow categories of equal size. For the first two distance categories (≤ 10 km, and >10 km and ≤ 20 km), we selected all the observations that fell within a density category, selecting from the distance category that had the fewest observations. We then randomly drew a subsample ($N = 174$ observations), balanced in terms of local density, from observations in the two distance categories and refitted the logistic regression model to this sample. Second, we also ran a model with density, including an interaction density–distance, and a model replacing distance by density everywhere in the model, to determine whether both density and distance were similar measures in terms of their effect on the probability of a female having cubs in a given year.

Model selection was based on the Akaike Information Criterion (AIC; Akaike 1974) using stepwise removal of model terms until the model with the lowest AIC value was reached. To achieve greater parsimony, we further reduced the resulting model by removing terms with effects that had P values > 0.1 . Preliminary analysis and diagnostics suggested a nonlinear relationship between the probability of a female having cubs and the distance to the nearest neighboring female. Hence, we first fitted distance to the nearest neighboring female using natural splines (piecewise cubic polynomials with smooth transitions) in a basic model with the predictors distance

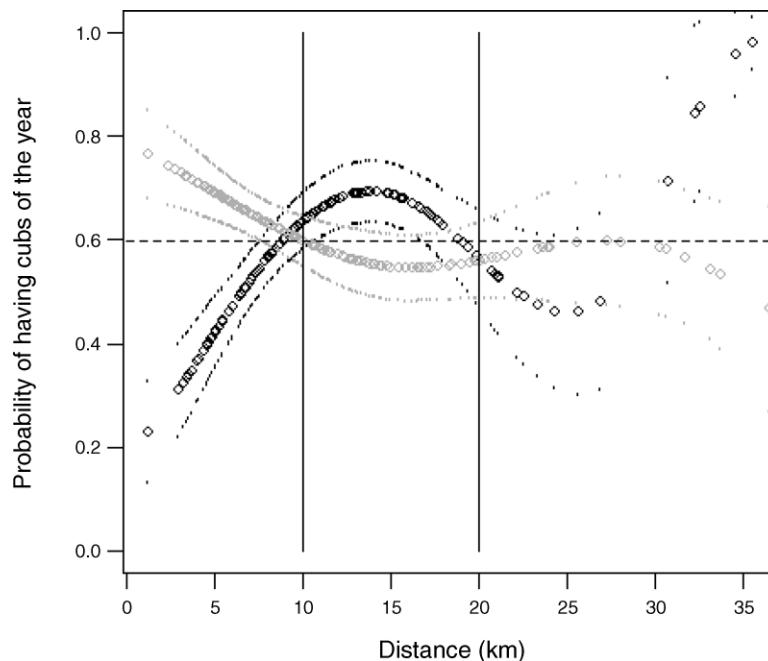


FIG. 1. Predicted probability of a female having cubs of the year and associated standard error boundaries from the logistic regression model with the effect of distance from the nearest neighboring adult female modeled as a natural spline (knots at 15 and 30 km). Predictions for females with nearest neighboring females that have cubs of the year are represented by large black circles, predictions for females with nearest neighboring females without cubs of the year are represented by large gray circles. Standard error limits are marked with small circles. The dashed line is a visual reference representing the mean annual probability of having cubs of the year (0.6) for our sample population.

to nearest neighboring female and the nearest neighboring female's reproductive status (having cubs of the year: yes or no), including the interaction between the terms. The best version of this model with splines based on AIC was one with knots at 15 and 30 km. After inspection of fitted values from this model, we selected cut points at 10 and 20 km for a categorical representation of distance.

We confirmed the goodness of fit of our logistic regression model with a binary response variable by using the Pearson residuals chi-square test (Hosmer et al. 1997, Crawley 2002).

We also checked for a potential lack of independence due to individual females that were used repeatedly in the model (as a result of testing over multiple years) by including bear identification as a random effect in a generalized linear mixed model version of our best model derived from model selection. We omitted the random effect from the final model because effect size estimates and their standard errors were nearly identical in the models with and without the random effect. We used the statistical package R 2.5 in all statistical analyses (*available online*).⁷

RESULTS

We obtained 335 pairings between female home-range centroids for the period 1987–2006 (dyads per female;

mean = 4.4, SD = 3.9, range = 1–16). The basic model with distance as a smoothing spline (Fig. 1) and the equivalent model with distance as a categorical variable (Fig. 2) provided nearly identical results. Because the model with distance from the nearest neighbor as a categorical variable had a lower AIC (Δ AIC of the model with splines = 5), we utilized the categorical representation of distance in the final model.

This model indicated an effect of the reproductive status (having cubs of the year; yes or no) of the nearest neighboring adult female, modulated by the distance between that female and the focal female, on a focal female's probability to have cubs in a given year. At distances ≤ 10 km, a female's odds of having cubs were on average 65.9% lower in years when her nearest neighboring female had cubs (Figs. 1 and 2). The effect of the reproductive status of the nearest neighboring female reversed at distances > 10 km and ≤ 20 km; females had 123.9% greater odds to have cubs when their nearest neighboring female also had cubs. The probability of having cubs for females whose centroids were separated from that of their nearest neighboring female by > 20 km to 40 km did not seem to be affected by their neighbor's reproductive status (Table 1). The model further showed differences in the probability of having cubs depending on age (the effect sizes are shown in Table 1). The probability of a female having cubs in the southern study area was higher than in the north

⁷ (<http://www.R-project.org>)

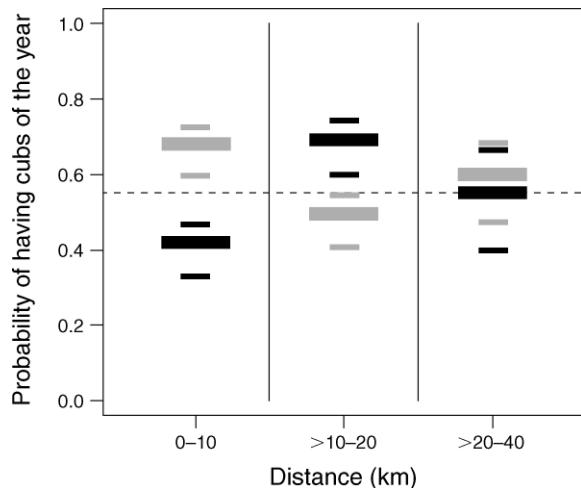


FIG. 2. Predicted probability of a female having cubs of the year (large horizontal bars) and associated standard error boundaries (small horizontal bars) from the logistic regression model with the effect of distance from the nearest neighboring adult female modeled as a categorical variable (cuts at 10 and 20 km). The figure shows the pattern for the most common age class in our study, 7–12-year-old females. Predictions for females with nearest neighboring females that have cubs of the year are represented by large black bars, predictions for females with neighbors without cubs of the year are represented by large gray bars. Standard error boundaries around the predicted probabilities are marked with small bars. The dashed line is a visual reference representing the mean annual probability of having cubs of the year (0.55) for 7–12-year-old females in our sample population.

(odds ratio = 1.62). Neither the nearest neighbor being the focal female’s mother nor the yearling condition index remained as predictors in the final model.

Distance to the nearest neighbor might be understood as a manifestation of density effects. However, after

balancing in terms of density and after its inclusion in the model, the effect that persisted qualitatively was the nearest neighbor’s reproductive status (with or without cubs) and its distance to the focal female; and its magnitude for the first distance category (<10 km separating centroids) actually increased ($\beta = -1.65$ density controlled vs. $\beta = -1.08$ without control). This suggests that the effect of distance to the nearest neighbor (and its reproductive status) that we obtained originally was indeed the appropriate measure in this study.

DISCUSSION

The probability of an adult female brown bear having cubs in a given year was significantly affected by the distance to the nearest neighboring female and whether or not she had cubs, and this effect was not just an effect of local density. The effect of distance to the nearest neighbor on female reproductive success has been found before (Mappes et al. 1995), but to our knowledge this is the first such finding in a wild population of a large, nonsocial mammal. In addition, we found that the pattern changed spatially. At short distances, ≤ 10 km between home-range centroids, a female was less likely to have cubs when her nearest neighbor had cubs. Ten km approximates the radius of a median home range of lone females in Scandinavia (217 km² in the south, 280 km² in the north; Dahle and Swenson 2003c, Støen et al. 2006a). Thus, at short distances there would be an extensive home-range overlap among the females. We suggest that reproductive suppression of subordinate females by dominant females causes this spatiotemporal pattern. In Scandinavia we have previously documented several phenomena suggesting female–female competition (see *Introduction*). Our findings are also in accordance with female-induced reproductive suppres-

TABLE 1. Results of the final logistic regression model of the effect of whether the nearest neighboring female had cubs of the year on the probability of a Swedish brown bear female having cubs of the year in a given year, depending on the distance separating home-range centroids of both animals.

Explanatory variables	β	SE	Z	Lci†	Odds ratio	Uci†	Pr(> Z)
(Intercept)	1.27	0.42	3.01	1.55	3.54	8.07	0.003
NNC‡, no	0.00						
NNC, yes	-1.08	0.33	-3.24	0.18	0.34	0.65	0.001
Distance, 0–10§	0.00						
Distance, 10–20	-0.76	0.36	-2.12	0.23	0.47	0.94	0.034
Distance, 20–40	-0.34	0.49	-0.70	0.27	0.71	1.86	0.486
Study area, north	0.00						
Study area, south	0.48	0.30	1.61	0.90	1.62	2.91	0.107
Age, 4–6 years	0.00						
Age, 7–12 years	-0.97	0.31	-3.13	0.21	0.38	0.70	0.002
Age, >12 years	-1.21	0.35	-3.45	0.15	0.30	0.59	<0.001
NNC, yes; distance, 0–10	0.00						
NNC, yes; distance, 10–20	1.88	0.52	3.62	2.37	6.57	18.20	<0.001
NNC, yes; distance, 20–40	0.88	0.74	1.20	0.57	2.42	10.25	0.232

Notes: The neighboring effect persisted for all age categories, but annual breeding probabilities were different depending on age. Model selection was based on AIC. The first level of each categorical variable served as the contrast for the remaining levels of that variable.

† Lci and Uci indicate lower and upper 95% confidence limits around the odds ratios, respectively.

‡ NNC, nearest neighbor had cubs of the year.

§ Distance categories expressed in km.



PLATE 1. Female brown bear with a yearling cub. Photo credit: I. Kojola.

sion found in many mammal groups (e.g., Digby 1995, Moellman and Hofer 1997, Wolff et al. 2002).

We propose that the mechanism involved for brown bears is a greater probability of encounter between two estrous females with overlapping home ranges, allowing one to dominate the other and suppress her estrus, rather than the probability of encounter between an estrous female and one with cubs. In our study areas, estrous females use large ranges in the mating season, suggesting that they roam to find mates, because these increased home ranges could not be explained by a seasonal change in food availability or by increased needs of estrous females to replenish body reserves after previous cub raising (Dahle and Swenson 2003*b*). The greater home-range sizes of estrous females would bring them into contact with more females, giving the opportunity for dominant females within hierarchies to suppress estrus in subdominant females (Støen et al. 2006*b*). The situation is quite different when female brown bears have cubs. They minimize their range size during the mating season, are spatially segregated from other bears after emerging from dens and, compared with estrous females during the mating season, females with cubs move shorter distances, are less active, and use different habitats (Dahle and Swenson 2003*b*, Swenson 2003, Ordiz et al. 2007). Thus, a dominant female with cubs would rarely meet a subdominant female during the mating season, greatly reducing the possibility for female-induced estrus suppression. Embryo loss and

neonatal mortality do not appear to be common in brown bears (Mano and Tsubota 2002); thus, if they mate, they are expected to have cubs.

The pattern reversed at greater distances between neighboring females, home range centroids at 10–20 km, and the probability of a female having cubs was higher when its nearest neighbor had cubs. We suggest that the reproductive suppression of subordinate females declines with increasing distance between females' home-range centroids, which allows synchronizing effects to become evident. Variation in food availability is one factor that might be expected to have a synchronizing effect on reproduction in brown bears, but including the environmental condition index did not significantly increase the model's ability to explain whether or not a female had cubs in a given year. Sæther et al. (1998) also found little environmental variation in the population growth rate of Scandinavian brown bears, suggesting that variation in food is not a major factor for reproduction in this population. Another synchronizing factor could be sexually selected infanticide (SSI), which is a major cause of bear cub mortality in parts of Scandinavia (Swenson et al. 1997, 2001) and is not correlated with food shortage (Swenson et al. 2001). Infanticide usually involves the killing of cubs that the perpetrating male has not fathered and shortens the time to the mother's next estrus (Swenson et al. 1997, Bellemain et al. 2006*a*). Presumably, several females with cubs could be affected simultaneously within the

home range of a perpetrating male, because males' home ranges are larger than those of females, and one male overlaps several females (Dahle and Swenson 2003c).

The lack of effect of a neighboring female having cubs beyond the distance of 20 km between females may be because that distance is too far for females to influence each other and infanticide by males to influence the reproduction of several females, if that was a synchronizing effect at intermediate distances (10–20 km between females). Male home range size is not large enough to influence several females >20 km apart, as the average radius of male home ranges in Scandinavia is ~16 km (Dahle and Swenson 2003c). Also, at distances >20 km apart we may have missed the true neighboring female more often.

The indication of reproductive suppression in brown bears suggests a mechanism for population regulation in the species. According to Wolff (1997), intrinsic population regulation can occur only in species in which females are territorial, offspring-rearing space is limited, and young females exhibit reproductive suppression. Wolff's model predicts that female territoriality, the threat of female infanticide, and the presence of male relatives in the natal home range are the proximate mechanisms for intrinsic population regulation in mammals. Agrell et al. (1998) summarized female mammals' counterstrategies to deter major losses in reproductive success provoked by infanticide. These strategies included aggression, female choice of dominant males, promiscuity to confuse paternity as defense against males, and territoriality, association with kin, and reproductive suppression as defense against females. Most of these strategies have been shown for Scandinavian bears, i.e., association with kin (Støen et al. 2005), female promiscuity, and choice of dominant males (Bellemain et al. 2006a, b), indications of territorial behavior (Dahle and Swenson 2003c, Støen et al. 2006a), and delayed primiparity possibly due to reproductive suppression (Støen et al. 2006b). Agrell et al. (1998) also included reproductive synchrony as a strategy to avoid loss of young caused by females. Although female-caused infanticide has been widely documented in mammals (e.g., Wolff 1993, Agrell et al. 1998), including brown bears (Hessing and Aumiller 1994, McLellan 1994), we consider it to be relatively uncommon in this species, because most of the known cases of infanticide were caused by males, and in our study areas, the three requirements of SSI were met (Bellemain et al. 2006a). Regardless, the threat of female-caused infanticide could delay reproduction by subdominant females until they could successfully rear offspring, as proposed for other species (Wasser and Barash 1983, Wolff 1997). However, female kin clustering and excluding nonkin, as observed in Scandinavian bears (Støen et al. 2005), also should reduce female infanticide by limiting interactions with unrelated females; each female in a kin cluster would maximize her inclusive fitness by not killing young related to her (Hodges et al. 2002). Based on

experiments, Ylönen et al. (1990) suggested that mutual familiarity decreased antagonism toward the juveniles, with positive consequences for their survival. Thus, kinship or mutual familiarity between neighboring females might decrease the frequency of infanticide (Ylönen et al. 1997), in accordance with the kin selection theory (Hamilton 1963). In our study areas, the relationship between genetic relatedness and geographic distance between female dyads was strongest within a distance of 40 km and then rapidly disappeared; that distance probably reflected the geographic distribution of closely related females (Støen et al. 2005). The thresholds found in this study, i.e., 10 and 20 km, are well below 40 km and include many related females.

The interval between consecutive litters is an essential reproductive parameter determining brown bear population growth rates (Eberhardt et al. 1994), so reduced reproductive success of young females may influence population regulation. Taylor et al. (1987) emphasized that bear cub production and cub and yearling survival were the most likely parameters to be reduced by density effects. Also, delayed sexual maturity of juveniles recruited into the population is one of the characteristics of increasing and high population densities, which may result from resource limitation or intrinsic, often female-induced, social stress (see Wolff et al. 2002). Bear density was higher in the south (30 bears/1000 km²) than in the north (11 bears/1000 km²; Zedrosser et al. 2006), but we accounted for the possible effects of both population and density, and it did not alter the reproductive pattern that we found. In this sense, the lower odds of females having cubs in the north were likely reflective of the longer interval between consecutive litters in the north than the south.

Female reproductive success varies with social rank in many gregarious mammals, including primates, ungulates, and carnivores (Holekamp et al. 1996). Reproductive suppression can occur by endocrine means, with preovulatory stages usually affected, or by behavioral mechanisms, and both types of suppression can be related (e.g., Creel and Macdonald 1995). The social and physiological mechanisms mediating reproductive suppression might be viewed as reaction norms to the social environment, perhaps with sociality in solitary carnivores being more flexible than commonly observed (Dalerum et al. 2006). The results from this study on wild, free-ranging brown bears, a solitary species commonly considered to be nonterritorial, show that social interactions and behavior of large mammals without an obvious form of social organization may be more similar to social species than previously assumed.

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