



Should I stay or should I go? Natal dispersal in the brown bear

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(Received 13 March 2006; initial acceptance 31 May 2006;

final acceptance 10 September 2006; published online 9 July 2007; MS. number: 8880)

We studied the causes of natal dispersal of male and female brown bears, *Ursus arctos*, in two study areas in Sweden. Males had a higher dispersal probability (94%) than females (41%). For males, we found no difference in dispersal probability or mean age of dispersal between the study areas, in spite of differences in population density and sex ratio. Male–male competition did not seem to influence subadult male dispersal probability significantly. These results support the inbreeding avoidance hypothesis as the cause of male natal dispersal. For females, dispersal probability decreased with increasing maternal age and decreased with increasing body size, and an interaction between maternal age and body size suggested that the importance of body size decreased with increasing maternal age. Nondispersing females were closer to their mother than their dispersing sibling sisters were in the period between weaning and dispersal. Female littermates seemed to compete for philopatry, suggesting that a dominance hierarchy among female littermates based on body size may cause the subdominant sister to disperse. If juvenile females are born into matrilineal assemblages, surrounded mostly by related females, the competition for philopatry may not be as severe as when they are born into an area surrounded by mostly nonkin females. This hypothesis is supported by the decreasing importance of body size for dispersal with increasing maternal age. We suggest that natal dispersal in juvenile female brown bears can be explained by the resident fitness hypothesis.

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Keywords: brown bear; inbreeding avoidance; natal dispersal; resident fitness; *Ursus arctos*

Dispersal often has multiple causes determined by different factors operating at different ontogenetic stages during an organism's life cycle (Ims & Hjermann 2001). In general, dispersing individuals of most bird and mammal species are young (Greenwood 1980). In contrast to birds, where dispersal is usually female biased, dispersal in mammals is often male biased and females remain philopatric (Pusey 1987).

Dispersal and philopatry can be viewed as behaviours of individual organisms that have demographic and genetic consequences for the population as a whole (Gaines & McClenaghan 1980; Armitage 1991; Byrom & Krebs 1999). Several hypotheses have been proposed to

explain the ultimate causes of natal dispersal in a wide range of species: the inbreeding avoidance hypothesis, where individuals disperse to avoid inbreeding with close relatives (Greenwood 1980; Cockburn et al. 1985; Pusey 1987; Wolff 1993, 1994); the intrasexual mate competition hypothesis, where individuals disperse to avoid competition for mates (Dobson 1982; Moore & Ali 1984); the resource competition hypothesis, where individuals disperse to increase access to environmental resources (Greenwood 1980; Waser & Jones 1983; Pusey 1987); and the resident fitness hypothesis, where juveniles compete for philopatry (Anderson 1989). However, the causes of dispersal can differ between species, between populations and between the sexes (Waser & Jones 1983; Moore & Ali 1984; Lidicker & Stenseth 1992), and the various proposed hypotheses are not mutually exclusive (Dobson & Jones 1985).

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We studied a solitary large carnivore, the brown bear, *Ursus arctos*, a species with a polygynous mating system (Schwartz et al. 2003; Bellemain et al. 2006). Natal dispersal in brown bears has been reported to be sex biased, with highly philopatric females establishing their home ranges in or adjacent to their natal areas and males dispersing long distances from their mother's home range (McLellan & Hovey 2001; Støen et al. 2006). Almost no female natal dispersal has been reported in brown bear populations in North America (e.g. McLellan & Hovey 2001), but 32–46% of females disperse from their natal home ranges in Scandinavian brown bear populations (Støen et al. 2006).

We examined a data series from a long-term study (20 years) of brown bears in two areas in Scandinavia. The study areas have different population densities (Zedrosser et al. 2006), and human influence (poaching) has resulted in a skewed sex ratio in one of the areas (Swenson et al. 2001a). These differences and the large geographical distance (600 km) between the study areas enabled us to use a 'quasiexperimental design' for our study. We defined a juvenile as a bear aged 1–4 years (both females and males), because the mean age at which bears had their first successful litter was 5 years in both study areas (Swenson et al. 2001a; Støen et al. 2006). Our aims were to investigate the causes of natal dispersal in brown bears, and also to examine which life history traits make individuals more prone to disperse. From the three main hypotheses to explain natal dispersal we made several predictions.

(1) Hypothesis 1: male brown bears disperse to avoid intrasexual mate competition (mate competition hypothesis). Because of the polygynous mating system of brown bears, females are unlikely to disperse to avoid mate competition, as has also been suggested for polygynous arctic ground squirrels, *Spermophilus* spp. (Dobson 1982; Byrom & Krebs 1999). The following predictions of the mate competition hypothesis therefore apply only to male brown bears: (1a) dispersal probability should be lower in the area with lower density and with fewer males per female (northern study area); (1b) mean dispersal age should be higher in the area with the uneven sex ratio (northern study area); and (1c) dispersal probability of juvenile males in both study areas should be positively related to the number of adult males in the vicinity of a given juvenile male.

(2) Hypothesis 2: juvenile male brown bears disperse to avoid inbreeding with close relatives (inbreeding avoidance hypothesis). Juvenile female brown bears disperse about 28 km from their natal area as 2–4 year olds in Scandinavia (Støen et al. 2006). Bellemain et al. (2006) found that 95% of all breeding brown bear pairs (i.e. a female and the father of her current offspring) were located within 40 km of each other in Scandinavia. Hence, dispersing juvenile females do not seem to settle in areas outside the reproductive reach of their father. However, inbreeding between philopatric females and their fathers does not seem to be a major problem in brown bears, because in our study areas only 2% of all litters resulted from incestuous matings between father and daughter (Bellemain et al. 2006). The following predictions of the

inbreeding avoidance hypothesis therefore apply only to male brown bears: (2a) there should be no differences in the probability of dispersal between the study areas, even with differences in density and sex ratio; (2b) mean dispersal age of juvenile males should not differ between the study areas; and (2c) dispersal probability of juvenile males in both study areas should not be related to the number of adult males in the vicinity of a given juvenile male.

(3) Hypothesis 3: juvenile female brown bears compete for philopatry (the resident fitness hypothesis). The prevalent hypothesis in the literature to explain the causes of female dispersal in mammals is the resource competition hypothesis, where individuals disperse to increase access to environmental resources, such as food or territories (Greenwood 1980; Waser & Jones 1983; Pusey 1987). However, female brown bears show some dispersal characteristics that argue against this hypothesis: related females form matrilineal assemblages, where members have more home range overlap than unrelated females (Støen et al. 2005). This implies that subadult females benefit from remaining philopatric, despite an increase in resource competition caused by the home range overlap.

Anderson (1989) formulated the resident fitness hypothesis as an ultimate explanation for dispersal in rodents. According to this hypothesis, it is selectively advantageous for adult female rodents to retain their maturing daughters near the natal site and to behave cohesively towards them, provided competition for essential resources is below the point at which these resources become limiting to the mothers' reproductive success. Sibling daughters should compete for philopatry, and the more dominant sibling is expected to force the subdominant sibling to emigrate (Wiggett & Boag 1992). Although formulated specifically to explain dispersal in rodents, the resident fitness hypothesis may fit the expectations of female brown bear dispersal better than the resource competition hypothesis does. Matrilineal assemblages in brown bears may be formed by philopatry or short-distance dispersal of juvenile female offspring (Støen et al. 2005). As more related females settle around a mother throughout time, this may decrease the competition with unrelated females. We therefore predicted from the resident fitness hypothesis that (3a) the probability of juvenile female dispersal should be negatively related to maternal age, when the effects of population density and environmental conditions are controlled; and (3b) the dispersal probability of juvenile females should be positively related to litter size and the number of female littermates, because competition for philopatry should increase with increasing litter size of females. If female offspring compete for philopatry, then physical advantages may influence the outcome; we therefore predicted that (3c) body size should be negatively related to dispersal probability. To assess whether there is competition among female littermates for philopatry, we predicted that (3d) in sibling pairs containing female dispersers and nondispersers, the nondispersing sibling should be geographically more closely associated with the mother than the dispersing sibling after separation but before dispersal.

METHODS

Study Area

We conducted the study in two areas in Scandinavia, separated by 600 km. The southern study area, hereafter named the south, was in Dalarna and Gävleborg counties in southerncentral Sweden (61°N, 18°E). The rolling landscape in the south is covered with coniferous forest, dominated by Scots pine, *Pinus sylvestris*, or Norway spruce, *Picea abies*, and contains a hunted bear population. The northern study area, hereafter named the north, was in Norrbotten County in northern Sweden (67°N, 18°E). The landscape is mountainous, with altitudes up to 2000 m with a subalpine forest dominated by birch, *Betula pubescens*, and willows, *Salix* spp., below the treeline and a coniferous forest of Scots pine and Norway spruce below the subalpine forest. The north contains three national parks, where hunting is not allowed; however, hunting is allowed in the surrounding forestlands. The areas differ also in the length of maternal care. In the south almost all cubs are weaned as yearlings, whereas in the north 40% of the litters are weaned as 2 year olds (Swenson et al. 1994; Dahle & Swenson 2003a). The two study areas differed in absolute population density (Støen et al. 2006; Zedrosser et al. 2006). The average density index was 11.1 bears/1000 km² in the north and 29.3 bears/1000 km² in the south (Støen et al. 2006). The study populations differed also in mortality regimes and in their male age structure (Swenson et al. 2001a). Bear hunting was allowed during the autumn in both areas, except in the national parks in the north; however, there was evidence of intensive poaching in the north (Swenson & Sandegren 1999). There were few adult males and very little male immigration in the northern area and a more evenly distributed male age structure in the south (Swenson et al. 2001a; Bellemain et al. 2006).

Capture, Handling and Radiotelemetry

All bears in this study were captured as a part of a long-term project on brown bear ecology in Scandinavia (e.g. Swenson et al. 1994, 1995, 2001a, b). Radiomarked female brown bears with yearling cubs were darted from a helicopter using a remote drug delivery system (Dan-Inject, Børkop, Denmark). For ethical reasons we did not capture females with cubs-of-the-year. The standard capture procedure was first to immobilize the yearling offspring and then the mother. We used helicopters because it is the only method that allows continual recapture of individuals. All captures were carried out in mid-April in the southern study area and in early May in the northern study area, shortly after the bears emerged from their winter dens, to avoid the danger of drowning (in open water) and high ambient temperatures. To avoid stress and physiological side-effects (hyperthermia) during immobilization, we kept intensive chasing well below 30 min. The average time from the initial sighting of an individual from the helicopter until it was fully immobilized was 8.4 min (J. E. Swenson, unpublished data). We used 2.5 mg of tiletamine, 2.5 mg of zolazepam and 0.02 mg

of medetomidine per kg body mass to immobilize the bears (Kreeger et al. 2002; Arnemo 2005; Arnemo et al. 2006). This drug combination is well tolerated by healthy bears (Arnemo 2005). Atipamezol was used as an antidote for medetomidine (5 mg per 1 mg of medetomidine; Kreeger et al. 2002).

A family group was always processed at the same location at the same time, and recovery from anaesthesia was timed so all individuals recovered at approximately the same time. An overall mortality rate of 0.3% was found for 892 captures during 1992–2004 (Arnemo et al. 2006). A circular sample of surface tissue (diameter 6 mm) was taken, with a sterile dermal biopsy punch, from an ear for genetic analysis. The head circumference (at the widest part of the zygomatic arch between eyes and ears) was measured with a tape measure and used as a measure of overall size of an individual. Because all bears were captured within a 2-week period in each study area, we did not adjust body size for capture date. We used VHF-radiotransmitters (model 500, Telonics Inc., Mesa, AZ, U.S.A.) for adult females (weight of the radiocollar: ca. 650 g; mass range of individuals: 50–140 kg). On all growing bears up to 3 years old, a breakaway zone was used on the radiocollar. Yearling brown bears were not fitted with a radiocollar because of their fast growth pattern and to avoid having to recapture them every year to change the radiocollar. Instead a sterile radiotransmitter (Telonics, model IMP/400/L HC) was implanted in their peritoneal cavity following a standard biomedical protocol (Arnemo 2005). Surgical anaesthesia was induced by the recommended immobilization drugs and dosages (Arnemo 2005; Arnemo et al. 2006), and the animal was injected with a long-acting combination of procaine penicillin and benzathine penicillin (PENI-kél L.A.15+15, Kela Laboratoria NV, Hoogstraten, Belgium) to reduce the risk of postoperative infection. The implants are removed as part of a long-term study of the effects of implants, following the same anaesthetic and surgical procedures (J. M. Arnemo, personal communication). From 1997 to 2005 we fitted 130 animals with implants and no complications associated with the surgery have been observed (J. M. Arnemo, personal communication).

Implants did not seem to have a negative effect on growth of yearling females; in a different study (Zedrosser et al. 2006) we found that body size of adult (≥ 4 years) female brown bears was influenced by population density and environmental conditions experienced when the females were subadults (1–3 years). Contrary to our expectations, we did not find a relation between yearling and adult female body size, which suggests that female brown bears are able to compensate for small yearling size with additional growth when they are subadults. This study contained several individuals that were implanted as yearlings, but were still able to show compensatory growth as a subadult (i.e. they were able to compensate for small yearling size; Zedrosser et al. 2006).

All capture and handling were approved by the appropriate Swedish ethical committee (Djuretiska nämnden i Uppsala). For further details regarding capture and handling of bears in our study refer to Kreeger et al. (2002), Arnemo (2005) and Arnemo et al. (2006). The bears were

located weekly by telemetry using standard triangulation methods from the ground or from an aircraft (helicopter or fixed-wing) during their nondenning period (Dahle & Swenson 2003b).

Definition of Dispersal

To identify individuals as dispersers or nondispersers we defined a juvenile as a disperser if it left its natal area and did not return before reproducing or reaching reproductive age (i.e. 4 years), or did not return within a minimum of 2 years (for those followed to reproductive age; see Støen et al. 2006 for a more detailed description). Natal areas of radiomarked bears were estimated as 95% minimum convex polygons (MCP) with the Ranges 6 computer package (Anatrack Ltd., Wareham, Dorset, U.K.). We estimated the natal areas for the offspring from all locations of the mother in the first 2 years of life and not only from positions when the mother was accompanied by the offspring. This was done for two reasons. (1) We obtained relatively few locations annually for each litter because of the long time between successive locations, the prolonged period (5–7 months) that bears spent in winter dens, and because using few locations underestimates home range sizes when using the MCP method (Macdonald et al. 1980). (2) We achieved a more reasonable estimate of the real home range the mother used when accompanied by the cubs by including all positions of the mother during the second year. To limit further underestimation of range size, we used only natal areas with more than 15 locations and, to reduce the effect of autocorrelation in the data, we used only locations separated by at least 100 h (Støen et al. 2006).

Individual Population Density Index

The population density around each individual (within a radius of 17.84 km, which corresponds to the density of bears per 1000 km²) was estimated in both the north and south, based on the high proportion of radiomarked bears and documented population growth rates (see Zedrosser et al. 2006 for a more detailed description). In the south, the population size was estimated from a DNA analysis of scats collected throughout the area in 2001 and 2002 (Bellemain et al. 2005). The individual density index around each radiomarked individual in our analysis was based on the location of individuals genetically identified by the scat sampling (71% of the radiomarked bears were represented in the scat samples, Bellemain et al. 2005), and the population growth rate (Sæther et al. 1998), which we used to correct the density estimate.

No corresponding population estimate was available for the north, but virtually every adult male and female and all subadult female bears were radiomarked (Swenson et al. 2001a). We used the locations of radiomarked bears, a correction to include the estimated number of subadult males, and data on growth rate of the population to calculate the individual density index as in the southern study area (Zedrosser et al. 2006).

Environmental Conditions Index

We used spring body mass of yearlings in a given year and study area as the basis to construct an index of the general environmental conditions for the study populations for each year. Rather than using the actual values and just controlling for sex (Garshelis 1994; Swenson et al. 2001b), we regressed yearling body mass as a function of maternal size, litter size, sex and individual population density. In this way we controlled for the variables that influence yearling mass independently of environmental conditions (Dahle et al. 2006). The standardized residuals from this regression were sorted by study area and year, and the average value for each year and area was then used as the index of environmental conditions for the year before the yearlings were weighed (Zedrosser et al. 2006). To estimate the effect of the individually experienced environmental conditions throughout the subadult period on dispersal behaviour, we averaged the indexes from age 1 to age 4 years (Zedrosser et al. 2006).

Statistical Analysis

Our first step was to fit a logistic regression model for the dispersal probability of both sexes, including both fixed and random effects, using the glmmPQL function in R 1.9.0 (R Development Core Team, Vienna, Austria). The logit function was used as a link function between the probability of dispersal and the linear expression of the regression variables. The fixed-effects variables of interest were study area, sex, yearling body size, internal relatedness, environmental conditions, litter size and maternal age, and we controlled for the effect of population density. In addition, the random effect of the mother was included to account for possible dependence in dispersal probability for siblings. This random effect induces a common positive correlation among all siblings. We used backward elimination for model identification.

We used a student's *t* test to test whether there was a difference in mean dispersal age of males between the northern and the southern study areas. A general linear model was used to test whether age at dispersal of males was influenced by the number of older males present within a 40-km radius around an individual male, while we controlled for the effects of body size and population density. This radius was chosen because 95% of all breeding pairs of brown bears were found within 40 km of each other in our study areas (Bellemain et al. 2006). We therefore considered a radius of 40 km as the potential area of influence by other males on natal male dispersal.

We used a paired *t* test to test whether females that at age 4 years were classified as nondispersers were geographically closer to their mother when they were yearlings than their female siblings that were classified as dispersers at the age of 4 years. We chose the yearling year to assess potential sibling competition, because females start to disperse as 2 and 3 year olds (Støen et al. 2006). We compared the distances between radiotelemetry positions of the mother, the nondispersing sibling and the dispersing sibling, taken on the same day. To reduce the effect of

autocorrelation in the data, we used only locations separated by at least 100 h.

We chose a level of $\alpha \leq 0.05$ for statistical significance. Sample sizes differed between the tests and models because of different selection criteria and the availability of variables. The statistical software R 1.9.0 was used in all analyses.

RESULTS

We analysed the dispersal probability of 48 individuals (16 males and 32 females) from 1989 to 2002. Of these individuals, 18 were from the northern (5 males, 13 females) and 30 (11 males, 19 females) from the southern study area. Males had a higher dispersal probability than females (Table 1): 15 (94%) of the 16 males dispersed and 13 (41%) of the 32 females dispersed. Maternal age and body size of the disperser as a yearling were negatively related to the probability of dispersal, but the interaction between these two variables indicates that the effect of yearling body size became less prominent with increasing maternal age (Table 1). The importance of body size was not due to larger body size of yearling males, because almost all of the males dispersed. Instead our result that smaller individuals were more likely to disperse was dependent upon female dispersal patterns. The following variables were removed from the analysis in this order: number of same-sex littermates ($\beta = -0.208$, $P = 0.757$), litter size ($\beta = 0.198$, $P = 0.832$), environmental conditions ($\beta = 0.209$, $P = 0.794$), study area ($\beta = 2.610$, $P = 0.213$), population density ($\beta = -0.052$, $P = 0.196$).

There was no significant difference in mean male dispersal age between the north and the south (south: $\bar{X} \pm SD = 2.08 \pm 0.70$ years; north: 2.45 ± 0.69 years; t test: $t_{34} = -1.483$, $P = 0.15$). The presence of older males did not influence juvenile male dispersal age significantly (general linear model: $\beta = -0.001$, $df = 15$, $P = 0.99$), when we controlled for body size ($\beta = -0.002$, $P = 0.51$), population density ($\beta = -0.0006$, $P = 0.48$) and study area ($\beta = -0.002$, $P = 0.62$).

Yearling females that did not disperse later on were significantly closer to the mother on a given day than their yearling female siblings that did disperse later (paired t test: mean distance between nondispersers and mother $\pm SD = 7.44 \pm 3.69$ km; mean distance between dispersers and mother $\pm SD = 10.08 \pm 3.69$ km; $t_{66} = 4.10$, $P < 0.001$; we used 67 simultaneous positions of 7 sister pairs from 5 litters with 12 individuals).

DISCUSSION

Male Natal Dispersal

We found that males had a higher dispersal probability than females. All but one males dispersed from their natal area. The higher dispersal probability in males is consistent with dispersal behaviour in other mammals (e.g. Pusey 1987; Nunes et al. 1997; Ferreras et al. 2004), including ursids (e.g. McLellan & Hovey 2001; Støen et al. 2006). In spite of differences in population density and sex ratio between the study areas, we found no difference in male dispersal probability (in support of prediction 2a as opposed to prediction 1a), because all but one males dispersed. There was also no difference in mean male dispersal age between the study areas (in support of prediction 2b as opposed to prediction 1b). These results support the inbreeding avoidance hypothesis as the cause of male natal dispersal in brown bears. The mean dispersal distance of 4-year-old males in Scandinavia was 119 km (Støen et al. 2006), which is sufficient for inbreeding avoidance, because 95% of the breeding pairs in Scandinavia were within 40 km of each other (Bellemain et al. 2006).

The number of males around a subadult male did not significantly influence dispersal probability (in support of prediction 2c as opposed to prediction 1c). In roe deer, *Capreolus capreolus*, subadult males with large antlers experience more aggression from resident males, and thus disperse more often (Wahlström 1994); in solitary felids such as the Florida panther, *Puma concolor coryi*, and the tiger, *Panthera tigris*, aggression by resident adult males towards subadults has been cited as the proximate cause of male dispersal (Smith 1993; Maehr et al. 2002). Our results suggest that male dispersal probability was not significantly influenced by male social structure. Antagonism by the mother and/or neighbouring females, as documented for example in Columbian ground squirrels, *Spermophilus columbianus* (Wiggett & Boag 1993), is probably not a cause of dispersal in male brown bears, because family breakup in brown bears is most often associated with the presence of an adult male during the mating season (Dahle & Swenson 2003c). In addition, most offspring are weaned as yearlings in Scandinavian brown bears, but the mean male dispersal age is older than 2 years. Because of this time interval between weaning and dispersal, maternal aggression seems to be an unlikely stimulus for male dispersal in brown bears.

Wolff (1993) reviewed 49 studies on natal dispersal in mammals, and found that it resulted from adult

Table 1. Results of a logistic regression model, including fixed and random effects, of the probability of dispersal in subadult brown bears

Explanatory variables	df	β	SE	t	P
Sex	27	-10.333	3.835	-2.694	0.012
Body size	27	-2.859	0.934	-3.061	0.005
Maternal age	27	-8.299	3.079	-2.695	0.012
Body size*maternal age	27	0.215	0.079	2.731	0.011

The random effect of the mother was included to account for possible dependence in dispersal probability for siblings. $N = 48$ (18 in the northern study area, 30 in the southern study area).

aggression in only four species. We were not able to identify any extrinsic motivating factors for dispersal of subadult male brown bears. Instead, much natal dispersal appears to have strong intrinsic components (Pusey 1987). The only nondispersing male reproduced with his mother, and both of these individuals had the same father (i.e. two-generational incest). This is the only known case of mother–son mating in our study among 107 known breeding pairs based on reproductive analyses (Bellemain et al. 2006).

Female Natal Dispersal

About 40% of the females in this study dispersed. As predicted from the resident fitness hypothesis, female natal dispersal probability decreased with both increasing maternal age (prediction 3a) and increasing body size (prediction 3c), but the interaction between maternal age and body size suggested that the importance of body size for dispersal probability decreases with increasing maternal age. We found no support for the prediction that litter size and the number of same-sex littermates influenced dispersal (prediction 3b). However, as predicted (prediction 3d), nondispersing sisters were closer to their mother after weaning than their dispersing sister. We interpret these results as support for the resident fitness hypothesis in explaining dispersal in juvenile female brown bears.

Our results suggest that the probability of female natal dispersal decreased with increasing maternal age, which may be related to the formation of matrilineal assemblages among brown bears. The increased overlap in a matriarchy indicates that related females are tolerant of each other (Støen et al. 2005), and related neighbouring individuals should be more likely than neighbouring nonkin females to facilitate philopatric behaviour of juvenile females. This tolerance in turn should decrease the probability of female natal dispersal. Older mothers should be surrounded by a higher number of related females than younger mothers; therefore the daughters of older mothers may face less antagonism. This implies that brown bears can distinguish between related and unrelated individuals. The mechanism behind kin recognition in brown bears is not known, but Mateo (2002) showed that Belding's ground squirrels, *Spermophilus beldingi*, produced odours that correlated with relatedness and Tegt (2004) showed that coyotes, *Canis latrans*, were able to recognize relatedness by using odour cues in faeces, urine, serum and anal sac secretions. Finally, the pattern of dispersal that we found may operate independently of density, because matrilineal assemblages were formed both in the core and the periphery of our study populations (Støen et al. 2005), which corresponded with high- and low-density areas of the brown bear distribution in Scandinavia (Swenson et al. 1998a, b; Dahle & Swenson 2003b).

Body size seems to be the factor deciding which females remain philopatric, because smaller individuals were more likely to disperse. Evidence from Columbian ground squirrels shows that daughters compete among themselves

for access to the natal site, because among nonparous siblings, the subordinate sisters appeared ultimately to emigrate (Wiggett & Boag 1992). Wiggett & Boag (1992) did not describe which factor(s) caused dominance or subordination in their study, but our results suggest that in brown bears this dominance hierarchy is based on body size. Craighead et al. (1995) have observed dominance hierarchies based on body size in adult brown bears at garbage dumps in Yellowstone National Park. Several studies evaluating the effect of size and condition on dispersal in mammals have found that larger individuals and those in better condition were more likely to disperse. Nunes & Holekamp (1996) reported that fat male Belding's ground squirrels dispersed earlier than lean males. In red deer, *Cervus elaphus*, stags the birth weight of dispersers was heavier than that of nondispersers (Clutton-Brock et al. 1982), and in roe deer dispersers were on average heavier than philopatric individuals (Wahlström & Liberg 1995). In contrast, Hanski et al. (1991) found that smaller individuals dispersed more frequently in the common shrew, *Sorex araneus*. However, the importance of body size for dispersal in female brown bears seems to decrease with increasing maternal age, perhaps because of the matrilineal assemblages. If juvenile females are born into an area surrounded mostly by related females, the competition for philopatry may not be as severe as if they are surrounded by mostly nonkin females.

Contrary to our predictions under the resident fitness hypothesis (prediction 3b), we did not find an effect of litter size or the number of female littermates on dispersal probability in female brown bears. This result is similar to that of Gundersen & Andreassen (1998), who were also unable to show that dispersal rates in root voles, *Microtus oeconomus*, were associated with litter size. Our negative result may be related to the small litter size of brown bears (on average 1.6–2.4 cubs per litter, McLellan 1994; Schwartz et al. 2003). However, there is indirect evidence for competition within litters in brown bears. Dahle et al. (2006) found that the body mass in yearling litters varied up to 29.5% between the heaviest and the lightest individuals. This suggests competition for maternal milk, which may establish a hierarchy among female siblings. Within-litter competition is also suggested by the finding in the present study that, after yearlings left their mother, the nondispersing sibling stayed closer to the mother than the female sibling that later dispersed.

Competition for philopatry implies that it is advantageous. Dahle et al. (2006) found suggestive evidence that natural mortality of subadult brown bears increases with decreasing yearling body size, which according to our results would suggest that dispersing individuals were at a higher risk. In a continuous bear population, dispersing daughters will experience competition from nonkin females. This could modify the cost-to-benefit ratio of philopatry versus dispersal and make the option of philopatry more attractive (Gundersen & Andreassen 1998). In addition, because bears are long lived (Schwartz et al. 2003), territory vacancies in a continuous population should be rare, and a dispersing female may find it difficult to move into a vacant area with sufficient habitat quality.

Acknowledgments

The Scandinavian Brown Bear Research Project was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Swedish Association for Hunting and Wildlife Management, WWF Sweden and the Research Council of Norway. We thank the research personnel in the Scandinavian Brown Bear Research Project for their assistance in the field. E. Bellemain carried out the genetic work. J. M. Arnemo, P. Wegge and B. Dahle provided useful comments on the manuscript. A.Z. was financially supported by the Austrian Science Fund project P16236-B06.

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