

Ole-Gunnar Støen · Andreas Zedrosser
Solve Sæbø · Jon E. Swenson

Inversely density-dependent natal dispersal in brown bears *Ursus arctos*

Received: 1 July 2005 / Accepted: 26 January 2006 / Published online: 18 February 2006
© Springer-Verlag 2006

Abstract There is considerable controversy in the literature about the presence of density dependence in dispersal. In this study, we exploit a data series from a long-term study (>18 years) on radio-marked brown bears (*Ursus arctos* L.) in two study areas in Scandinavia to investigate how individual-based densities influence the probability of natal dispersal and natal dispersal distances. Cumulatively, 32% and 46% of the females and 81% and 92% of the males dispersed before reaching 5 years of age in the northern and southern study area, respectively. Density had a negative effect on both the probability of dispersal and dispersal distances for the dispersing animals, when controlling for study area, sex and age, making this the first study to show that natal dispersal probability and distances are inversely density dependent in a large carnivore. We suggest that female–female competition for space caused females in higher density areas to settle closer to their natal area. For males, however, merging of demes, resulting in decreased relatedness and increased heterozygosity in an expanding population, might be the reason for shorter dispersal distances in males living at higher densities. This has been hypothesised for small mammals. The high proportion of dispersing female brown bears in Scandinavian compared with North American studies

might be due to lower densities in Scandinavia and recent population expansion, with unoccupied areas available at the edges of the population. The longer dispersal distances in female Scandinavian brown bears suggest less social constraints on movements than for North American females. The longer dispersal distances by Scandinavian males may be due to increased searching for potential mates in peripheral areas with lower densities of females. These results, in addition to results of other brown bear studies, suggest that brown bears might be more territorial than previously thought, and that density is regulated by social interactions.

Keywords Dispersal behaviour · Dispersal distance · Population density · Population expansion · Scandinavia

Introduction

Dispersal has important implications for population ecology and conservation through redistribution of animals. The most common mechanism of population redistribution in space is the movement of young animals, because the distance moved and proportion of animals moving are commonly larger in subadults than adults in both birds and mammals (Greenwood 1980; Dobson 1982; Gese and Mech 1991; Paradis et al. 1998; Nelson and Mech 1999).

There is abundant evidence that the dispersal rate increases with increasing competition for limiting resources. However, there has been considerable controversy in the literature about the presence of density dependence in dispersal (Lambin et al. 2001). Both positive and inverse density dependence has been demonstrated, perhaps reflecting that emigration and immigration show contrasting responses to density (Lambin et al. 2001). Several studies have shown that emigration is more likely to occur at high population densities (Fonseca and Hart 1996; Hertzog 1995). However, other studies have found evidence for inverse

Communicated by Diethart Matthies

O.-G. Støen (✉) · A. Zedrosser · J. E. Swenson
Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences,
P.O.Box 5003, 1432, Ås, Norway
E-mail: ole.stoen@umb.no
Tel.: +47-64-965800
Fax: +47-64-965801

A. Zedrosser
Institute for Wildlife Biology and Game Management,
Department for Integrative Biology, University of Natural
Resources and Applied Life Sciences, Wien, Austria

S. Sæbø
Department of Chemistry, Biotechnology and Food Science,
Norwegian University of Life Sciences, Ås, Norway

density dependence in emigration, and also an even clearer negative relation between density and immigration (Wolff et al. 1988; Woodroffe et al. 1995; Blackburn et al. 1998; Lambin 1994a; Andreassen and Ims 2001). The social fence hypothesis predicts an inverse density dependence of dispersal, due to increased aggression within and among groups, and thus inhibition of immigration and emigration at high densities relative to carrying capacity (Hestbeck 1982).

Density-dependent dispersal is probably a widespread process and models have shown that density-dependent dispersal strategies almost always evolve (Travis et al. 1999) and might affect population dynamics of spatially structured populations and the probability of local extinction in source-sink populations (Jost and Brandl 1997; Amarasekare 2004; Lecomte et al. 2004). However, density-dependent dispersal has been the subject of relatively few empirical studies, possibly because wide ranges of population densities are rarely encountered over the relatively short duration of many intensive field studies (Sutherland et al. 2002). Thus, many of the studies and models on density-dependent dispersal are based on small mammals and insects in patchy environments and metapopulations (Midtgaard 1999; Albrechtsen and Nachman 2001; Lambin et al. 2001; Amarasekare 2004).

The brown bear (*Ursus arctos* L.) is a solitary carnivore with a promiscuous mating system (Pasitschniak-Arts 1993; Schwartz et al. 2003; Bellemain et al. 2005a). Males have larger home ranges than females, but both males and females have intra- and inter-sexually overlapping home ranges (Pasitschniak-Arts 1993; Dahle and Swenson 2003a). Dispersal in brown bear populations has been reported to be sex-biased, with highly philopatric females establishing their breeding home ranges in or adjacent to their natal areas and males dispersing long distances from their mothers' home range (Glenn and Miller 1980; Blanchard and Knight 1991; McLellan and Hovey 2001; Kojola et al. 2003). The Scandinavian brown bear population has increased in numbers and expanded in range from four small remnant areas after their near extirpation around 1930 to encompass more than half of Sweden and parts of Norway, today (Swenson et al. 1994; 1995). A previous study using data from hunter-killed bears concluded that pre-saturation dispersal exists in the Scandinavian brown bear (Swenson et al. 1998), suggesting that dispersal in brown bears is either density independent or inversely density dependent.

Wolff (1997) predicted that dispersal distances should be longest at low densities in territorial species, because emigrants should experience the least resistance and lowest cost. Boonstra (1989) and Lambin (1994a, b) found that dispersers moved shorter distances at higher densities in Townsend voles (*Microtus townsendii*), but to our knowledge no published studies have described how density influences dispersal distances in large mammals.

In this study, we exploit the data series from a long-term study (> 18 years) on brown bears in Scandinavia to investigate how individual-based densities influence

the probability of natal dispersal and natal dispersal distances. In this paper, we define natal dispersal as the permanent movement out of the natal area. We attempted to determine whether the probability of dispersal in brown bears was related to density and, if so, in which way. Because brown bears are generally not considered to be territorial (Pasitschniak-Arts 1993; Schwartz et al. 2003), we predicted that dispersal distance is density independent.

Materials and methods

Study area

This study was conducted in two study areas in Scandinavia, separated by 600 km. The southern study area, hereafter named the south, was in Dalarna and Gävleborg counties in south-central Sweden and Hedmark County in southeastern Norway (61°N, 18°E). The northern study area, hereafter named the north, was in Norrbotten County in northern Sweden (67°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*), whereas in the north the landscape is mountainous, with altitudes up to 2,000 m and subalpine forest dominated by birch (*Betula pubescens*) and willows (*Salix* spp.) below the tree line and coniferous forest of Scots pine and Norway spruce below the subalpine forest. Both study areas are described in Dahle and Swenson (2003a).

Natal areas, dispersal and distance calculations

During 1984–2001, 326 different bears were captured with helicopters (203 in the south and 123 in the north), of which 284 were radio-marked (172 in the south and 112 in the north). Offspring of radio-marked females were first captured as yearlings. Age of bears not followed from birth was estimated by counting the annuli on a cross-section of a premolar root (Matson et al. 1993). The bears were radiomarked and located weekly during their active period using standard triangulation methods from the ground or the air (Dahle and Swenson 2003a). Dispersing bears were followed until death or radio-transmitter failure; some were followed far beyond the areas where bears were captured. The methods used to capture, mark and radiotrack bears are described by Dahle and Swenson (2003b).

To determine whether dispersal occurred, natal areas were estimated as 95% minimum convex polygons (MCP) with the Ranges 6 computer package (Anatrack, 52 Furzebrook Rd., Wareham, Dorset, UK). A 95% MCP was used to avoid the influence of unusual forays and because MCP is the most frequently reported home range estimate reported in brown bear literature (Schwartz et al. 2003). Most brown bear family groups (mother and offspring) break up during the mating

season in June–July when the cubs are 1.5 years old, but some may stay with their mother for a longer period (Dahle and Swenson 2003b). Because female brown bears are reported to be highly philopatric, we used conservative criteria to define dispersers. A bear was defined as a disperser if it left its natal area and did not return before reproducing or reaching reproductive age, or did not return within a minimum of 2 years, for those where monitoring ceased before reproduction or reaching reproductive age. Five years was used as the reproductive age for both females and males, because mean age of first successful litter is 5 years both in the south and in the north (Swenson et al. 2001; Bellemain 2004). We had data from only 1 year after leaving the natal area for some bears, which could not be classified according to these criteria. These bears were categorised as dispersers only if the dispersal distance exceeded the mean dispersal distance of dispersers of the same sex and age with all locations outside the natal area for two or more active seasons.

An underestimation of the size of a natal area could possibly overestimate the number of dispersers using these criteria. We therefore estimated the natal areas based on all locations of the mother in the 2 first years of life for the offspring and not only from positions when accompanied by the offspring. This was done because of two reasons: (1) relatively few locations were obtained annually for each litter due to the long time between successive locations, the prolonged period (5–7 months) spent in winter dens, and because using few locations underestimates home range sizes when using the MCP method (Macdonald et al. 1980); and (2) a 95% MCP underestimates the real home ranges of brown bears. By including all positions of the mother in the second year, we achieved a more reasonable estimate of the real home range the mother used when accompanied with the cubs. To further limit underestimation of range size, only natal areas with >15 locations were used (Fig. 1). To reduce the effect of autocorrelation in the data, only locations separated by at least 100 h were used. Because animals that are dispersing do not have a defined home range, according to the home range definition by Burt (1943), the dispersal distance was measured from the arithmetic mean centre of the natal area to the median distance of all the annual positions. Thus, only locations outside the natal area were used in this analysis. When calculating the proportions of dispersed bears in different age classes, animals that were lost (e.g. radio-transmitter failure or died) before denning were removed from the analysis for the year when monitoring ceased.

Individual population density index

North

From 1995 to 2002, virtually every adult male and female and all subadult female bears were radio-marked in our northern study area (Swenson et al. 2001). We

calculated the arithmetic mean of the radio locations of every radio-marked bear in the year 2002 (the year with most radio-marked individuals). We then counted the number of centres of these adult males, adult females and subadult females in the year 2002 that were within a distance of 17.84 km from the annual arithmetic mean centres of all radio-marked bears throughout the entire study period. We chose a radius of 17.84 km because it approximates an area of 1,000 km² commonly used as the basis of density measure for bears (McLellan 1994); the median adult male home range was 833 km² in this area (Dahle and Swenson 2003a). The number of cubs present per adult female was estimated by dividing the mean litter size in our northern study area (2.4; Swenson et al. 2001) by the mean litter interval (2.6 years; Swenson et al. 2001), which resulted in estimated 0.92 cubs present per adult female per year. Because no radio-marked subadult males were represented in the initial count of bears surrounding a given individual, we multiplied the number of subadult females by 2, assuming an even sex ratio (Bellemain 2005b). The individual density index I_d per 1,000 km² was calculated as $I_d = n_{ad,m} + 1.92n_{ad,f} + 2n_{subad,f}$ where $n_{ad,m}$ is the number of radio-marked adult males, $n_{ad,f}$ is the number of radio-marked adult females and $n_{subad,f}$ is the number of radio-marked subadult females. We subtracted the area within the 17.84-km radius around a bear that extended beyond the borders of our study area using the software ArcView GIS 3.2a (Environmental Systems Research Institute, 1992–2000), and extrapolated the number of bears to an area of 1,000 km².

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

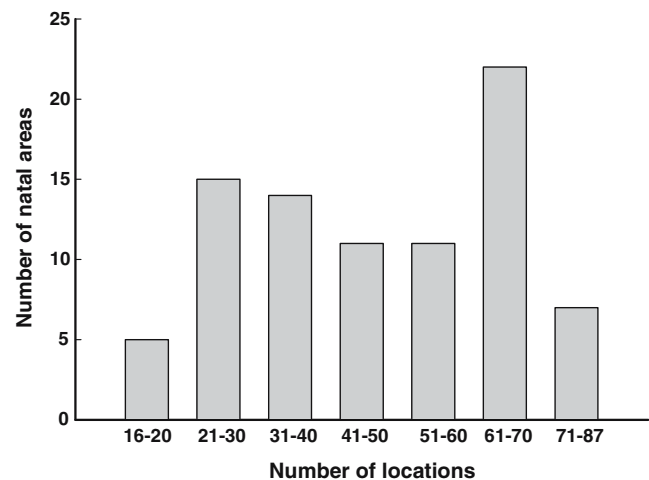


Fig. 1 Histogram of the number of locations used in the estimation of 85 brown bear (*Ursus arctos* L.) natal areas in Scandinavia

The temporally corrected individual density index tI_d for an individual bear in year y (for $y < 1995$) was then $tI_d = I_d / 1.14^{(1995-y)}$, where I_d is the individual density index for 1995–2002. The estimates of individual population density indices in both study areas rely on the assumption that the spatial distribution obtained in 2002 (northern study area) and 2001–2002 (southern study area, see below) reflect the spatial distribution in both study areas over the entire study period.

South

A population size estimate, based on a DNA analysis of non-invasive sampling of scats, was carried out in the southern study area in 2001 and 2002 (Bellemain 2005b). We have used these results as a basis to calculate an individual density index around each individual in our analysis. For each radio-marked bear, we counted the number of genetically identified individuals within a 17.84-km radius, based on the centres of the locations of all scat samples for each individual. The median adult male home range was 1,055 km² in this area (Dahle and Swenson 2003a). Bellemain et al. (2005b) found that 71% of all radio-marked bears in the southern study area were represented in the genetic sample. To account for the individuals not detected in the non-invasive population sampling, we divided the individual density index by 0.71. The resulting individual density index I_d thus can be expressed as $I_d = n_i / 0.71$, where n_i is the number of genetically identified individuals surrounding a radio-marked bear. We subtracted the area within the 17.84 km radius around a bear that extended beyond the borders of our study area, and extrapolated the number of bears to a density of 1,000 km², as in the northern study area.

Sæther et al. (1998) estimated a population growth rate of about 16% annually in our southern study area for the period 1985–1995. Population size and density estimates based on aerial capture-mark-recapture techniques were carried out in the southern study area in 1993 (Swenson et al. 1995) and again in 2001 (Solberg 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 similar in the period 1993–2001. To temporally correct the individual population density indices for this period, we assumed stable densities from 1993 to 2002. The temporally corrected individual population density index tI_d for an individual bear in year y (for $y < 1993$) was then $tI_d = I_d / 1.16^{(1993-y)}$, where I_d is the index for 2001–2002.

Statistical analysis

A logistic regression model for dispersal, including both fixed and random effects, was fitted using the `glmmPQL` function in R (the MASS library) (R Development Core

Team 2005). The logit function was used as link function between the probability of dispersal and the linear expression of the regression variables. The fixed effects variables of interest were density, study area, sex, year and age. In addition, the random effect of the mother was included to account for possible dependence in dispersal probability for siblings. The random effect induces a common positive correlation among all siblings. For several individuals, there are repeated observations of dispersal/non-dispersal, and ideally an additional random term for individual should be included in the model to account for this dependence. However, when the fixed effect of age is included in the model, a situation known as “complete separation” arises, under which the maximum-likelihood estimates for the fixed effects do not exist. In our case, this means that a perfect fit of the model can be accomplished by letting the variance of the individual random term be sufficiently large and the estimate of the age effect approach infinity. This is because no animal can be both dispersed and non-dispersed at a given age. Hence, a random term for individual cannot be included in the model, and the estimated effects of the fixed covariates will therefore be at the population level rather than at the individual level. Neuhaus et al. (1991) showed that omitting a random intercept term in a logistic model reduces the magnitude of the estimated regression coefficients. This means that the true effects at the individual level are probably larger (in absolute value) than those found in our analysis.

The dispersal distances of the animals defined as dispersers were analysed by means of a linear mixed model. Dispersal distances were log-transformed (natural log) before analyses to meet assumptions of normality and equal variance among groups of data (Sokal and Rohlf 1995). The effects of density, area, sex, year and age on the log-distances were estimated by means of restricted maximum likelihood to account for the random effects in the model. As for the analysis of dispersal probability in the logistic model, the random effect of mother was included to account for possible dependencies among sibling. In addition the random effect of the individual bear was included, because there were repeated observations of individuals. Due to this random effect, all observations on each animal will be equally correlated. Two-tailed tests were used and an α level of 0.05 was selected for statistical significance. The model fit was evaluated by investigating residual plots.

Results

Natal home ranges were calculated for 178 animals (89 females and 89 males) from 85 litters produced by 41 different mothers. These bears were followed for a total of 595 bear-years (353 female and 242 male bear-years). An average of 48 ± 19 (mean \pm SD) locations were used for the calculation of 85 natal home ranges using 95% MCP and the average area of the natal home ranges was 257 ± 157 km². There was a tendency for the natal areas

in the north to be larger than in the south, when controlling for the identity of the mother ($F_{1,39}=2.61$, $P=0.08$). Of the 178 animals, 54 (18 females and 36 males) were classified as dispersers at some time during their first 4 years of life, whereas 75 (51 females and 24 males) did not disperse before monitoring ceased. Forty-nine animals had too few locations to be classified as dispersers or non-dispersers.

Cumulatively, 32% and 46% of the females and 81% and 92% of the males dispersed before reaching 5 years of age in the north and south, respectively (Table 1). The average density index value for bears per year was 11.1 ± 8.9 bears/1,000 km² in the north and 29.3 ± 18.9 bears/1,000 km² in the south. When controlling for all the other factors, density had a negative effect on the probability of dispersal (Table 2). Bears in the south were more prone to disperse than bears in the north and age had a positive effect on dispersal probability (Table 2). There was a significant interaction between age and sex in the probability to disperse (Table 2), most likely because most males dispersed as 2-year-olds, whereas most females dispersed as 3-year-olds (Fig. 2). The insignificant sex effect was retained in the model, because the interaction between age and sex was significant.

The longest dispersal distances recorded were 90 km for a female and 467 km for a male. When controlling for all the other factors density had a significant negative effect on the dispersal distances (Table 3). Separate analyses for the two study areas gave similar results (results not shown), indicating that the slight difference in methods for density estimation in the two study areas was not crucial for the conclusions in the global model. The animals in the south had longer dispersal distances than those in the north and there were significant effects of sex, age and the interaction between sex and age (Table 3). Due to the chosen coding of the sex variable (0 for males and 1 for females), the positive and significant age effect is the effect of age on dispersal distances for males. The estimated interaction effect between age and sex gives the additional contribution of females to the age effect. Because the interaction effect is negative, the age effect for females is smaller than for males. The

positive effect of sex merely indicates that females disperse farther than males at age 0, which is of no biological interest. The significant negative interaction between sex and age indicates longer dispersal distances for males than females for all ages above 1 year (Fig. 3).

Discussion

We found that the natal dispersal probability and dispersal distances were inversely density dependent in brown bears in Scandinavia. Density-dependent dispersal has been observed in small mammals and ungulates (Boonstra 1989; Jones 1986; Lambin 1994a, b; Linnell et al. 1998; Andreassen and Ims 2001), but this is the first study to show that natal dispersal probability is inversely density dependent also for a large carnivore. Among badgers, a medium-sized carnivore, there seems to be a lower male dispersal rate (i.e. emigration into new groups) in populations with high density compared to low density populations, although female immigration did not correlate with density (Woodroffe et al. 1995). The inverse density-dependent dispersal probably contributes to an increased spatially heterogeneous abundance of brown bears in the landscape. Because brown bears are spatially structured in matrilineal assemblages (Støen et al. 2005), this might lead to a spatial variation in population dynamics within the population and among matrilineal lines, as seen in other species and theoretical studies (Jost and Brandl 1997; Lecomte et al. 2004; Ims and Andreassen 2005).

Theoretical models supported by empirical data predict that dispersal should be density independent in non-territorial mammals and inversely density dependent in territorial species (Wolff 1997). Dahle and Swenson (2003a) found that home range sizes of both male and female brown bears were inversely related to population density in Scandinavia. Støen et al. (2005) found that overlap of home ranges in female brown bears in Scandinavia was positively related to relatedness, indicating that brown bears recognize kin and tolerate kin more than non-kin. These results, in addition to the results in this study, suggest that brown bears might be

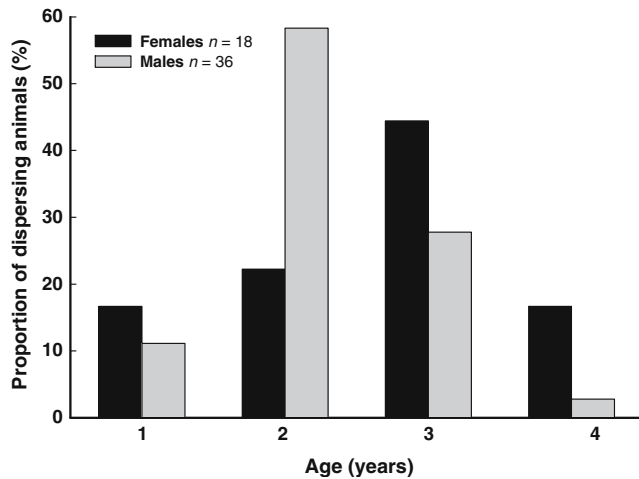
Table 1 Observed and cumulative proportions of Scandinavian brown bears (*Ursus arctos* L.) dispersing by sex and age in two study areas in Sweden

Area	Age (years)	Dispersal at a given age (%)		Cumulative dispersal (%)	
		Males (n)	Females (n)	Males	Females
North	1	0.0 (25)	8.3 (24)	0.0	8.3
	2	38.9 (18)	0.0 (19)	38.9	8.3
	3	37.5 (8)	12.5 (16)	61.8	19.8
	4	50.0 (2)	15.4 (13)	80.9	32.1
South	1	11.4 (35)	2.5 (40)	11.4	2.5
	2	60.9 (23)	13.3 (30)	65.3	15.5
	3	77.8 (9)	30.0 (20)	92.3	40.9
	4	0.0 (0)	9.1 (11)	92.3	46.2

Table 2 Logistic regression model of the effects of density, study area, sex and age on the probability of dispersal by brown bears during ages 1 through 4 years, including both fixed and random effects

Explanatory variables	β	SE	df	t	P
Density	-0.0361	0.0144	310	-2.5039	0.012
Area	1.8489	0.5552	32	3.3303	0.002
Sex	0.4720	0.8966	310	0.5265	0.6
Age	1.9417	0.3235	310	6.0028	<0.001
Sex \times age	-1.0721	0.3759	310	-2.8518	0.005

The global model included: whether not dispersed or dispersed (0 or 1) as a response variable ($n=348$), density, study area (north = 0, south = 1), sex (male = 0 and female = 1), year, age, and all possible two-way interactions as explanatory variables, and mother identity as a random effect. After a successive exclusion of the least significant terms, but keeping main effects if included in a significant two-way interaction, the final model included the variables presented in the table

**Fig. 2** Age when dispersing Scandinavian brown bears permanently left their natal areas

more territorial than previously thought, and that density is regulated by social interactions. Emigration rates of juveniles from their natal sites over a range of densities have been documented in only a few studies of territorial mammals and all have shown that emigration rates decrease when densities are high (Wolff 1997).

This is the first study to show that density has a negative effect on dispersal distances in a large mammal. Cockburn (1985) hypothesised that males in expanding populations should move shorter distances from their natal site at high than at low densities to avoid

inbreeding, because of shorter distance between unrelated animals and increased heterozygosity due to successful migration and fusion of demes. We found this pattern in both males and females. Following Cockburn (1985), this might be the reason for the effect for males, but we do not believe the observed effect was due to inbreeding avoidance for females. Female dispersers moved on average 27.6–28.4 km from the centre of their natal area as 2- to 4-year-olds, which is shorter than the 95% distribution of geographic distances between reproductive pairs, which approximated 40 km deduced from parentage analysis (Bellemain et al. 2005a). This means that females would not settle in areas outside the reproductive reach of their father. However, males dispersed on average 118.9 km as 4-year-olds, which is three times this distance, and most likely resulted in avoidance of inbreeding. Boonstra (1989), found a similar effect, i.e. shorter dispersal distances at high density in female meadow voles (*Microtus pennsylvanicus*), and concluded that it was female–female competition for space that caused females in higher density areas to settle closer to their natal area. We suggest that this also occurs in brown bears.

The dispersal distance could be biased towards shorter distances due to the difficulty in following long distance dispersers (Rehmeier et al. 2004). Ten (9 males and 1 female) of the 54 dispersing brown bears were lost (i.e. lost collar or radio transmitter failure) and never located again during the study. Only four of these animals had moved longer than the average dispersal distance for the sex and age when disappearing, indicating

Table 3 Linear mixed model of the effects of density, study area, sex and age on the dispersal distance by brown bears during ages 1 through 4 years, including both fixed and random effects

Explanatory variables	β	SE	df	t	P
Density	-0.0270	0.0042	124	-6.4916	<0.001
Area	0.5082	0.2078	20	2.4454	0.024
Sex	0.5549	0.2347	31	2.3645	0.025
Age	0.7607	0.0618	124	12.3050	<0.001
Sex \times age	-0.3992	0.0859	124	-4.6500	<0.001

The global model included: natural log of dispersal distance as a response variable ($n=181$), and density, study area (north = 0, south = 1), sex (male = 0 and female = 1), year, age, and all possible two-way interactions as explanatory variables, and mother identity and individual identity as random effects. After a successive exclusion of the least significant terms, but keeping main effects if included in a significant two-way interaction, the final model included the variables presented in the table

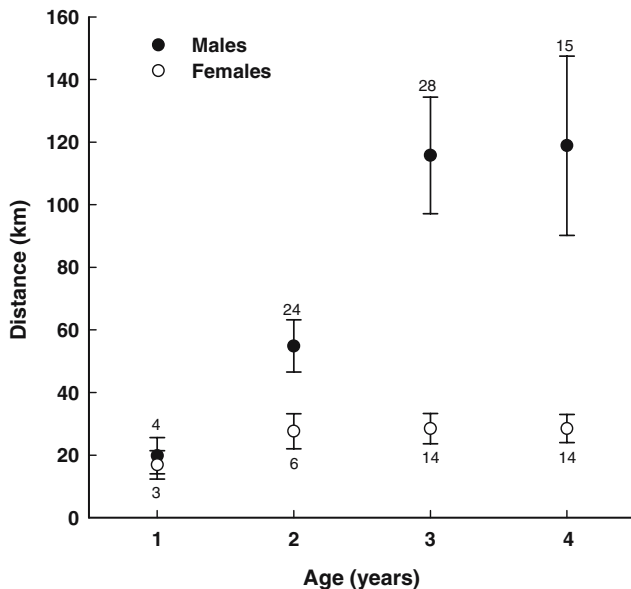


Fig. 3 Mean distance (± 1 SE) from the centre of the natal area to annual locations of the Scandinavian brown bears that dispersed from the natal area. The numbers above and below error-bars give the number of observations in each age and sex class

that the loss of long distance dispersers due to detection problems was probably not a major bias in this study. The detection probability was high, possibly because the long dispersers often came into populated areas or areas with livestock and were shot as part of the management regime.

Bears in the south were more prone to disperse, and dispersed longer than bears in the north. The trend towards larger natal home ranges in the north ($P=0.08$) might explain this effect, because our criteria for dispersal assumed no overlap with the natal area. In areas with the same movement pattern but larger home ranges, our criteria would result in fewer dispersers. The shorter dispersal distances in the north can also be explained by poaching, because a large proportion of the bears moving outside the study area in the north are killed illegally (Swenson and Sandegren 1999), thus biasing the dispersal distances towards shorter distances. The lower dispersal probability at a given density in the north may be explained by differences in carrying capacity, which should be lower in the north due to lower primary productivity, i.e. less food per unit area for brown bears, which is also suggested by the greater home ranges. Thus, there might be less dispersal in the north with the same absolute density, because the area might be saturated with bears in the north at a lower absolute density than in the south.

The Scandinavian brown bears showed a sex-biased dispersal, and the difference between sexes increased with age, with more males dispersing than females and males moving farther. This is consistent with the general pattern in mammals, where females generally are philopatric and males disperse (Greenwood 1980; Dobson 1982; Pusey 1987). This has also been shown in other

studies of brown bears (Glenn and Miller 1980; Blanchard and Knight 1991; McLellan and Hovey 2001; Kojola et al. 2003).

Even with our conservative criteria for defining dispersers, 32% and 46% of the females had left their natal area by the age of 4 years in the two study areas, respectively (Table 1). This is in clear contrast to the strong female philopatry that has been reported in North American populations of brown bears (Glenn and Miller 1980; Blanchard and Knight 1991; McLellan and Hovey 2001). In Yellowstone National Park, USA, all three brown bear females tracked from family break-up had home ranges that overlapped with their natal areas (Blanchard and Knight 1991). McLellan and Hovey (2001) reported from British Columbia, Canada, that ten female brown bears from known mothers that were tracked to adulthood still had some locations inside their mothers' home ranges when 4 years of age. According to our criteria, these females would not have been classified as dispersers.

McLellan and Hovey (2001) reported dispersal distances without distinguishing between dispersers and non-dispersers. To compare dispersal distances between Scandinavia and British Columbia, the distance between the arithmetic means of natal areas and annual locations for all bears (both dispersers and non-dispersers) were calculated. These calculations revealed that both males and females dispersed farther in Scandinavia than in British Columbia. Sixteen males and 31 females moved an average of $108.3 \text{ km} \pm 27.4$ (mean \pm SE) and $15.7 \text{ km} \pm 2.4$, respectively, in Scandinavia, compared to 23.5 ± 1.7 for 5 males and 6.8 ± 2.5 for 10 females in British Columbia (McLellan and Hovey 2001). The observed differences between Scandinavia and British Columbia may be due to differences in densities in relation to carrying capacity between the two areas. The brown bear density in British Columbia was increasing from an estimated $57/1,000 \text{ km}^2$ in 1981 to $80/1,000 \text{ km}^2$ in 1986, which is high for an interior population (McLellan 1989) and more than twice the average density observed in this study in Scandinavia. The remarkably high proportion of dispersing females in the Scandinavian populations might be due to the fact that the population was expanding and unoccupied areas were available at the edges of the population. The longer dispersal distances in Scandinavian female brown bears might also indicate fewer social constraints on movements than for North American females. However, the longer dispersal distances by Scandinavian males may be due to an increased searching for potential future mates in peripheral areas, which have lower densities of females (Swenson et al. 1998).

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, the Norwegian Institute for Nature Research, WWF Sweden, the Research Council of Norway and 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 Ole Wiggo Røstad and John Gunnar Dokk for technical assistance in data handling, and Jonas Kindberg for help with GIS calculations. We also thank Andrew Derocher, Svein Dale, Per Wegge, Harry P. Andreassen, Thor S. Larsen, Bjørn Dahle, Eva Bellemain and Andrés Ordiz for commenting on earlier drafts of the manuscript. All capture and handling of bears reported in this paper complies with the current laws regulating the treatment of animals in Sweden and Norway and were approved by the appropriate management agencies and ethical committees in both countries.

References

- Albrechtsen B, Nachman G (2001) Female-biased density-dependent dispersal of a tephritid fly in a fragmented habitat and its implications for population regulation. *Oikos* 94:263–272
- Andreassen HP, Ims RA (2001) Dispersal in patchy vole populations: role of patch configuration, density dependence and demography. *Ecology* 82:2911–2926
- Amarasekare P (2004) The role of density-dependent dispersal in source-sink dynamics. *J Theor Biol* 226:159–168
- Bellemain E (2004) Genetics of the Scandinavian brown bear (*Ursus arctos*): implications for biology and conservation. PhD thesis, Agricultural University of Norway, Ås
- Bellemain E, Zedrosser A, Manel S, Waits LP, Taberlet P, Swenson JE (2005a) The dilemma of female mate selection in the brown bear, a species with sexually selected infanticide. *Proc R Soc B*. DOI 10.1098/rspb.2005.3331
- Bellemain E, Swenson JE, Tallmon DA, Brunberg S, Taberlet P (2005b) Estimating population size of elusive animals using DNA from hunter-collected feces: comparing four methods for brown bears. *Conserv Biol* 19:150–161
- Blackburn GS, Wilson DJ, Krebs CJ (1998) Dispersal of juvenile collared lemmings (*Dicrostonyx groenlandicus*) in a high-density population. *Can J Zool* 76:2255–2261
- Blanchard BM, Knight RR (1991) Movements of Yellowstone grizzly bears. *Biol Conserv* 58:41–67
- Boonstra R (1989) Life history variation in maturation in fluctuating meadow vole populations (*Microtus pennsylvanicus*). *Oikos* 54:265–274
- Burt WH (1943) Territoriality and home range concepts as applied to mammals. *J Mammal* 24:346–352
- Cockburn A (1985) Does dispersal increase as populations expand? *Oikos* 44:367–368
- Dahle B, Swenson JE (2003a) Home ranges in adult Scandinavian brown bears *Ursus arctos*: effect of mass, sex, reproductive status, population density and habitat type. *J Zool* 260:329–335
- Dahle B, Swenson JE (2003b) Family break-up in brown bears; are young forced to leave? *J Mammal* 84:536–540
- Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Anim Behav* 30:1183–1192
- Fonseca DM, Hart DD (1996) Density-dependent dispersal of black fly neonates is mediated by flow. *Oikos* 75:49–58
- Gese EM, Mech LD (1991) Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. *Can J Zool* 69:2946–2955
- Glenn LP, Miller LE (1980) Seasonal movement of an Alaskan Peninsula brown bear population. *Int Conf Bear Res Manag* 4:307–312
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162
- Hertzog AL (1995) Effects of population density on long-distance dispersal in the goldenrod beetle *Trirhabda virgata*. *Ecology* 76:2044–2054
- Hestbeck JB (1982) Population regulation of cyclic mammals: the social fence hypothesis. *Oikos* 39:157–163
- Ims RA, Andreassen HP (2005) Density-dependent dispersal and spatial population dynamics. *Proc R Soc Lond B* 272:913–918
- Jones WT (1986) Survivorship in philopatric and dispersing kangaroo rats (*Dipodomys spectabilis*). *Ecology* 67:202–207
- Jost K, Brandl R (1997) The effect of dispersal on local population dynamics. *Ecol Model* 104:87–101
- Kojola I, Danilov PI, Laitala H-M, Belkin V, Yakimov A (2003) Brown bear population structure in core and periphery: analysis of hunting statistics from Russian Karelia and Finland. *Ursus* 14:17–20
- Lambin X (1994a) Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's vole (*Microtus townsendii*). *Ecology* 75:224–235
- Lambin X (1994b) Sex ratio variation in relation to female philopatry in Townsend's voles. *J Anim Ecol* 63:945–953
- Lambin X, Aars J, Pieltney SB (2001) Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) *Dispersal*. Oxford University Press, Oxford, pp 164–182
- Lecomte J, Boudjemadi K, Sarrazin F, Cally K, Clobert J (2004) Connectivity and homogenisation of population sizes: an experimental approach in *Lacerta vivipara*. *J Anim Ecol* 73:179–189
- Linnell JDC, Wahlström K, Gaillard J-M (1998) From birth to independence: birth, growth, neonatal mortality, hiding behaviour and dispersal. In: Andersen R, Duncan P, Linnell JDC (eds) *The European roe deer: the biology of success*. Scandinavian University Press, Oslo, pp 257–283
- Macdonald DW, Ball FG, Hough NG (1980) The evaluation of home range size and configuration using radio tracking data. In: Amlaner CJ, Macdonald DW (eds) *A handbook on biotelemetry and radio tracking*. Pergamon Press, Oxford, pp 405–422
- Matson GM, van Daele L, Goodwin E, Aumiller A, Reynolds HV, Hristienko H (1993) A laboratory manual for cementum age determination of Alaskan brown bear first premolar teeth. Matson's Laboratory, Milltown
- McLellan BN (1989) Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. *Can J Zool* 67:1856–1860
- McLellan B (1994) Density-dependent population regulation of brown bears. In: Taylor M (ed) *Density-dependent population regulation in black, brown, and polar bears*. International conference on bear research and management, Monograph Series No. 3, pp 15–24
- McLellan BN, Hovey FW (2001) Natal dispersal of grizzly bears. *Can J Zool* 79:838–844
- Midtgaard F (1999) Is dispersal density-dependent in carabid beetles? A field experiment with *Harpalus rufipes* (Degeer) and *Pterostichus niger* (Shaller) (Col., Carabidae). *J Appl Entomol* 123:9–12
- Nelson ME, Mech LD (1999) Twenty-year home-range dynamics of a white-tailed deer matriline. *Can J Zool* 77:1128–1135
- Neuhauser GD, Kalbfleisch JD, Hauck WW (1991) A comparison of cluster-specific and population averaged approaches for analyzing correlated binary data. *Int Stat Rev* 59:25–36
- Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. *J Anim Ecol* 67:518–536
- Pasitschniak-Arts M (1993) *Ursus arctos*. *Mammal Species* 439:1–10
- Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol Evol* 2:295–299
- R Development Core Team (2005) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Rehmeier RL, Kaufman GA, Kaufman DW (2004) Long-distance movements of the deer mouse in tallgrass prairie. *J Mammal* 85:562–568
- Sæther BE, Engen S, Swenson JE, Bakke Ø, Sandegren F (1998) Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates. *Oikos* 83:403–416
- Schwartz CC, Miller SD, Haroldson MA (2003) Grizzly bear. In: Feldhammer GA, Thompson BC, Chapman JA (eds) *Wild*

- mammals of North America: biology, management and conservation, 2nd edn. The John Hopkins University Press, Baltimore, pp 556–586
- Sokal RR, Rohlf FJ (1995) Biometry. Freeman, New York
- Solberg KH, Bellemain E, Drageset O-M, Taberlet P, Swenson JE (2006) An evaluation of field and non-invasive genetic methods to estimate brown bear (*Ursus arctos*) population size. *Biol Conserv* 128:158–168
- Støen O-G, Bellemain E, Sæbø S, Swenson JE (2005) Kin-related spatial structure in brown bears, *Ursus arctos*. *Behav Ecol Sociobiol* 59:191–197
- Sutherland WJ, Gill JA, Norris K (2002) Density-dependent dispersal in animals: concepts, evidence, mechanisms and consequences. In: Bullock JM, Kenward RE, Hails RS (eds) *Dispersal ecology*. Blackwell, Oxford, pp 134–151
- Swenson JE, Sandegren F, Bjärvall A, Söderberg A, Wabakken P, Franzén R (1994) Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. *Biol Conserv* 70:9–17
- Swenson JE, Wabakken P, Sandegren F, Bjärvall A, Franzén R, Söderberg A (1995) The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies in Norway and Sweden. *Wildl Biol* 1:11–25
- Swenson JE, Sandegren F, Söderberg A (1998) Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *J Anim Ecol* 67:819–826
- Swenson JE, Sandegren F (1999) Mistänkt illegal björnjakt i Sverige. In: Bilagor till Sammanhållen rovdjurspolitik; Slutbetänkande av Rovdjursutredningen. Statens Offentliga Utredningar 1999:146 (in Swedish), Stockholm, pp 201–206
- Swenson JE, Sandegren F, Brunberg S, Segerström P (2001) Factors associated with loss of brown bear cubs in Sweden. *Ursus* 12:69–80
- Travis MJJ, Murrell DJ, Dytham C (1999) The evolution of density-dependent dispersal. *Proc R Soc Lond B* 266:1837–1842
- Wolff JO (1997) Population regulation in mammals: an evolutionary perspective. *J Anim Ecol* 66:1–13
- Wolff JO, Lundby KI, Baccus R (1988) Dispersal, inbreeding avoidance and reproductive success in white-footed mice. *Anim Behav* 36:456–465
- Woodroffe R, MacDonald DW, da Silva J (1995) Dispersal and philopatry in the European badger, *Meles meles*. *J Zool* 237:227–239