

# Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal

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## Summary

1. The distribution of brown bears (*Ursus arctos* L.) expanding into suitable habitat in Sweden following near extermination was estimated using harvest data from the period 1981–93. Core areas were defined as female concentration areas, where 90% of the hunter-killed females were taken.

2. Three predictions were tested, based on results of earlier bear dispersal studies, which show that females are extremely philopatric. Prediction 1: the relative density of females declines more rapidly from the centre of a core area towards the edge than for males. Prediction 2: males dominate in the peripheral areas, especially males in the age of most active dispersal (2–4 years of age). Prediction 3: females in the periphery are found closer to the edge of the core area than males.

3. The results of the present study supported Predictions 1 and 2, but not Prediction 3. This indicates that males were more prone to disperse from the core areas than females. However, females that did disperse did not differ from males in distance from the core areas, and females were found up to 80–90 km from them. Such long-distance female dispersal has apparently not been previously documented in other bear populations that are stable or declining. The results strongly suggest that presaturation dispersal, i.e. dispersal occurring before the carrying capacity of the habitat has been reached, is occurring in this increasing population. This phenomenon might be more common in increasing populations of large mammals than was previously thought. Regarding conservation of bears, this result is positive for gene flow and meta-population dynamics and negative for livestock losses in formerly bear-free areas.

4. Core and peripheral areas can be identified based on the age and sex of shot bears. This allowed us to classify Norway as a peripheral area. Bear density appears difficult to estimate near an expansion front because of large differences in densities over short distances.

**Key-words:** brown bear, population expansion, presaturation dispersal, Sweden, *Ursus arctos*.

*Journal of Animal Ecology* (1998) **67**, 819–826

## Introduction

How a population expands its range is influenced by the dispersal of individuals, by population growth, and by temporal and spatial variation in the environmental factors that affect dispersal and population growth (Lubina & Levin 1988). Other factors influencing the dispersal of individuals include population size in relation to ecological carrying capacity, the breeding system, taxonomic group, etc. (Sinclair 1992). Perhaps as a result of these sources of variation, expansion is manifested differently among mammalian species; for example, the expansion front is very steep in the coyote

[*Myocastor coypus* (Molina)] (Usher 1986) and the sea otter (*Enhydra lutris* L.) (Lubina & Levin 1988), but is flat, as a result of long-distance dispersal, in the North American mink (*Mustela vison* Schreber) (Usher 1986), raccoon dog (*Nyctereutes procyonoides* Gray) (Helle & Kauhala 1991) and Eurasian beaver (*Castor fiber* L.) (Hartman 1995). Understanding how a native species increases from low population levels to recolonize former habitats, and the underlying mechanisms, is important to conserve the species and predict the consequences of increase in areas where small populations still exist. One example of such a species is the brown bear (*Ursus arctos* L.).

The authors of the present study were unable to find published studies describing how an increasing bear population expands in distribution. In stable or declining populations, dispersal of brown bears and black bears (*U. americanus* Pallas) is sex-biased, with males usually dispersing far and females establishing their home ranges in or near their mother's home range (Alt 1978; Glenn & Miller 1980; Rogers 1987; Blanchard & Knight 1991; Schwartz & Franzmann 1992; Reynolds 1993). Rogers (1987) considered female dispersal in black bears to be uncommon and, when they did disperse, they moved only to the nearest available area. Young female bears appear to be so philopatric that dispersal of females to adjacent areas where females have been removed has been considered to be minimal (Schwartz & Franzmann 1992; Reynolds 1993).

This description of dispersal is not consistent with the geographical expansion of brown bears that has occurred in Scandinavia. Brown bears survived in only four small areas in Sweden following an extermination attempt, and as few as 130 may have been present at the population low in the 1930s (Swenson *et al.* 1995). Since then, the population has increased rapidly, and the distributional range now covers over half of Sweden and some of adjacent Norway (Taberlet *et al.* 1995), although females are concentrated in four geographically large (9700–23 500 km<sup>2</sup>) areas (Swenson *et al.* 1994). This raises the question of whether bears exhibit presaturation dispersal, i.e. dispersal occurring before the carrying capacity of the habitat has been reached (Lidicker 1975). This was first described for small mammals (Krebs *et al.* 1973) and has been most commonly observed in this group of mammals (Stenseth & Lidicker 1992). Sinclair (1992) expected it not to be found in large mammals, except in expanding populations, and even then it would be rare. However, it has been described in several larger mammals, including wild boar (*Sus scrofa* L.) (Janeau & Spitz 1990), roe deer (*Capreolus capreolus* L.) (Wahlström & Liberg 1995), European badger (*Meles meles* L.) (Cheeseman *et al.* 1988) and red fox (*Vulpes vulpes* L.) (Trehella, Harris & McAllister 1988; Allen & Sargeant 1993). Whether or not presaturation dispersal occurs in bears has several ramifications. If it does occur, it will add a new group, large carnivores, to the growing list of mammals exhibiting presaturation dispersal, which increases the need for a general explanation. The knowledge will allow better prediction of future range increase and, more importantly, it can provide insight that is important for bear conservation; for example, many populations of bear species are declining, apparently as a result of human exploitation, habitat loss and habitat fragmentation (Servheen 1990). Species showing presaturation dispersal may be more successful in coping with habitat fragmentation (Lidicker & Koenig 1996), which suggests that it may be more important to focus on human exploitation and habitat loss than habitat frag-

mentation *per se* if presaturation dispersal is common in bears.

The aim of this study is twofold. First, the question was asked 'Is there evidence for presaturation dispersal of female brown bears in the increasing Scandinavian population?'. Based on the literature on bear dispersal, the answer is 'no'. Therefore, the null hypothesis is that presaturation dispersal does not occur. The change in occurrence and relative density of male and female brown bears in Sweden is documented in relation to the distribution of concentrations of females. Results are compared with three predictions of the null hypothesis. Prediction 1: the density of females declines more steeply from the centre of female concentration areas (termed core areas here) than for males, because of the extreme philopatry of females. The more shallow decline for males would be expected because of their propensity to disperse widely. Prediction 2: males predominate in the peripheral area surrounding the core areas, especially males in the age of most active dispersal, 2–4 years of age (Reynolds 1993; J.E. Swenson & F. Sandegren, unpublished observations). Prediction 3: females in the periphery are, on average, closer to the core areas than the males because of short dispersal distances in females (Rogers 1987; Schwartz & Franzmann 1992; Reynolds 1993). This is an extreme and conservative test of the third null hypothesis, because females could show presaturation dispersal even though dispersing shorter distances than males.

The second aim of this study, if results determine that differences can be detected in the sex and age structure of bears in core compared with peripheral areas, is that this difference should be useful to identify core and peripheral areas elsewhere. Results from Sweden are tested on data from bears killed in Norway because of the controversy about whether the brown bears in Norway constitute a core population or only the periphery of a population. Kolstad *et al.* (1986) estimated the 1983 population in Norway to be 160–230 individuals in 17 definable populations and reported that reproduction had been documented in 13 of these populations. Elgmork (1988) criticized this latter work, concluding that the brown bear was a threatened species at extremely low densities in Norway. Similarly, Swenson *et al.* (1995) considered the bears in Norway to be few in number and to comprise only a peripheral part of the large and expanding Swedish population.

## Methods

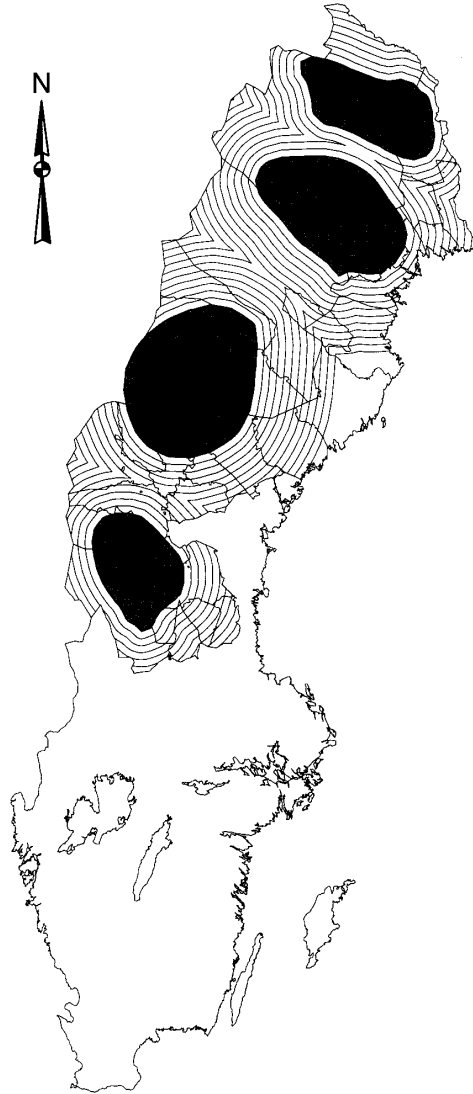
Relative densities of hunter-killed brown bears within the areas open to hunting in Sweden during 1981–93 were used to describe the change in density of males and females in relation to four female concentration areas, or core areas, from which the population is growing (Swenson *et al.* 1994). A core area was defined as the 90% harmonic mean area of hunter-killed

females (Dixon & Chapman 1980; Kenward 1987). From the edge of each of these core areas, concentric zones, 10 km in width, were constructed both into and out from the edge (Fig. 1). The areas outside the core boundary were defined as peripheral. For analyses corresponding zones were combined for each of the core areas, and only the first seven zones into the core areas from the boundaries were considered because

these were available for all four core areas (Fig. 1), and because the study was interested in analysing general patterns, not area-specific patterns. The annual home ranges of bears probably included several zones, as the home range diameter for an adult female brown bear in Sweden is about 24 km, based on an average size of 460 km<sup>2</sup>, calculated by the convex polygon method, for 52 annual home ranges. Adult males in the core areas had an average home range diameter of about 44 km (1507 km<sup>2</sup>,  $n = 26$ ), whereas it was about 99 km in the peripheral areas (7760 km<sup>2</sup>,  $n = 7$ , Wabakken *et al.* 1992).

It is mandatory for bear hunters in Sweden to report the kill of bears to the authorities and to provide location of kill, sex, mass and several biological samples, including one premolar tooth, to the bear research project. In the present study, the locations for each sex were overlaid upon the map of the zones and the number killed in each zone during the period 1981–93 was obtained. The area of each zone was also calculated. However, not all municipalities were open to hunting during the entire 13-year period, nor was 100% of the area in each municipality open to hunting (Swenson *et al.* 1994). To correct for this, the area open to hunting in each municipality was multiplied by 0.077 (1/13) for each year for which bear hunting was allowed. If an entire municipality was open every year, the resulting area would equal the area of the municipality. Each zone comprised parts of many municipalities, and each municipality contributed to many zones, which reduced area-specific biases in the analysis based on zones (Fig. 1). Estimates of the area open to hunting for each year were obtained from the county offices of the Swedish Hunters' Association. Some areas were closed to bear hunting because of administrative regulations, the prohibition of hunting bears in national parks, or decisions by large land owners, such as timber companies. A Geographic Information System (ArcInfo) was used to calculate the corrected areas of each zone.

Using the corrected area, the numbers of females, males and the total killed annually per 1000 km<sup>2</sup> open to bear hunting were calculated and defined as relative density. This provides an accurate estimate of the relative distribution of bears in relation to the core areas, especially when the data for all four core areas are combined, because the system of bear hunting in Sweden did not significantly constrain the location of kill, especially within the combined zones. In Sweden, a special hunting license is not required to hunt bears; all hunters with the right to hunt on an area and who have a gun that is powerful enough to be allowed for bear hunting may shoot a bear if the area is open for hunting. The harvest is regulated by area-specific quotas (Swenson *et al.* 1994). As a result, a great number of hunters can legally kill a bear if they see one. In fact, most hunters that shot bears during the study years were not specifically hunting for bears; for example, 62% of the bears shot during 1981–89 were killed



**Fig. 1.** Areas in Sweden open to brown bear hunting during at least some years in the period 1981–93. Shown are the four core areas (shaded), based on 90% harmonic mean areas of hunter-killed female bears, 10-km wide concentric zones extending into the core areas and into the peripheral area starting from the boundaries of the core areas, and the borders of the municipalities in which bear hunting was allowed. Southern Sweden, in white, was closed to bear hunting during the entire study period.

incidentally by moose (*Alces alces* L.) hunters (Dahlström 1990). Thus, the distribution of the kills should reflect the distribution of bears. The sex ratio of harvested bears in Sweden is not significantly different from 50:50 (Swenson *et al.* 1994). The sex ratio of harvest was considered to be a reflection of the sex ratio of the living bears in an area, recognizing that males are generally more vulnerable to harvest (Bunnell & Tait 1981). In addition, females with young are protected in Sweden, which reduces the vulnerability of adult females to harvest.

Most bears killed in Norway were killed as a management action following heavy losses of domestic sheep in an area. The wildlife management authorities issue a kill permit and a specified group of hunters is given the task of killing the bear.

Age of killed bears was estimated by counting the annuli on a cross-section of a premolar root (Craighead, Craighead & McCutchen 1970). These teeth were provided by hunters, but only a few teeth were available from the beginning of the study.

To test for differences in frequency data, exact homogeneity tests with 10 000 simulations were utilized. Throughout this study, one-tailed statistical tests were used when the direction of the difference was expected, based on the published literature.

## Results

As expected from Prediction 1, the relative density of bears declined rapidly from the centres of the core areas toward the edges (Table 1, Fig. 2). The relative

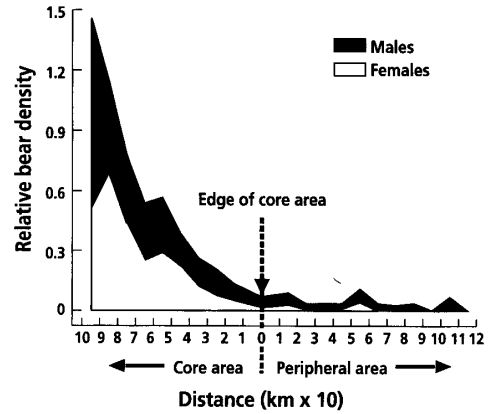


Fig. 2. Cross-section of the generalized expansion front of the increasing brown bear population in Sweden, showing relative densities of males (black) and females (white) along a gradient from the centre of the core areas to far out into the periphery. Relative densities are based on hunter-killed bears (Table 1), and zones are illustrated in Fig. 1.

density data were transformed into natural logarithms and the change in relative density was analysed from the 60–70 km zone inside the core area to the edge of the core area (Fig. 1). The slopes were statistically less than 0 for females ( $r = -0.963$ , d.f. = 5, two-tailed  $P = 0.0005$ ), males ( $r = -0.977$ , d.f. = 5,  $P = 0.0002$ ), and for total bears ( $r = -0.982$ , d.f. = 5,  $P = 0.0001$ ). The decline in relative density was significantly steeper for females ( $\beta = -0.361 \pm 0.045$

Table 1. Relative densities of harvested brown bears in Sweden during 1981–93 in relation to 10-km wide zones in core areas and peripheral areas. Relative density is defined as bears killed by hunters per 1000 km<sup>2</sup> open to hunting per year

Area type	Distance from edge	Corrected area (km <sup>2</sup> )	Harvest		Relative density		
			Males	Females	Males	Females	Total
Core	80–100	746	9	5	0.942	0.516	1.458
	70–80	1539	9	14	0.450	0.700	1.150
	60–70	2960	13	17	0.338	0.442	0.780
	50–60	5149	19	17	0.284	0.254	0.538
	40–50	8436	30	32	0.274	0.292	0.566
	30–40	12288	26	36	0.163	0.225	0.388
	20–30	14328	26	23	0.140	0.123	0.263
	10–20	15915	27	16	0.131	0.077	0.208
	0–10	17263	20	10	0.089	0.045	0.134
Periphery	0–10	17884	12	4	0.052	0.017	0.069
	10–20	18314	14	7	0.059	0.029	0.088
	20–30	16132	6	1	0.029	0.005	0.034
	30–40	14846	5	2	0.026	0.010	0.036
	40–50	13073	4	2	0.024	0.012	0.036
	50–60	10702	9	2	0.065	0.043	0.108
	60–70	8690	4	0	0.035	0.000	0.035
	70–80	6015	2	1	0.026	0.000	0.026
	80–90	3629	1	0	0.021	0.013	0.034
	90–100	2173	0	0	0.000	0.000	0.000
	100–110	1124	1	0	0.068	0.000	0.068
> 110	3189	0	0	0.000	0.000	0.000	

SE) than males ( $\beta = -0.222 \pm 0.022$ ,  $t = 2.78$ , d.f. = 10,  $P = 0.02$ ). The relative density of females was halved every 19 km from the centre of a core area towards the edge, for males every 31 km, and for all bears every 24 km ( $\beta = -0.284$ ).

In agreement with Prediction 2, 75% (58) of the 77 bears shot outside the core areas were males, compared to 51% (179) of 349 shot in the core areas. This difference was statistically significant ( $\chi^2 = 14.8$ , d.f. = 1, one-tailed  $P < 0.0001$ ). The sex ratio within the core areas did not differ from the expected 50:50 ratio ( $\chi^2 = 0.23$ , d.f. = 1, two-tailed  $P = 0.66$ ), but it did differ from it in the peripheral areas ( $\chi^2 = 19.7$ , d.f. = 1, one-tailed  $P < 0.0001$ ).

The males killed in the peripheral area had a different age structure than those killed in the core areas, also consistent with Prediction 2. The males in the 2- to 4-year age classes comprised 46% of the 33 males with determined age in the peripheral areas, compared with 24% among 86 males with determined age in the core areas ( $\chi^2 = 5.0$ , d.f. = 1, one-tailed  $P = 0.01$ , Table 2). Age determination was only available for 8 females killed in the periphery. No differences were evident between female age structure in core and peripheral areas ( $\chi^2 = 0.91$ , d.f. = 1, two-tailed  $P = 0.67$ , Table 2).

According to Prediction 3, females in the peripheral area were expected to have been closer, on average, to the core area boundaries than males. This prediction was rejected, as there was no significant difference in distance from the edge of the core area between the sexes (Mann-Whitney  $U$ -test,  $U = 479$ ,  $n = 58$  males and 19 females, one-tailed  $P = 0.19$ , Table 1). Females were found in every peripheral zone to 50–60 km from the boundary of the core area, and one was killed 80–90 km distant from it (Table 1, Fig. 2). Males were found in every zone out to 80–90 km, and one was killed 100–110 km from the boundary (Fig. 2).

During the period 1973–93, 30 brown bears were killed in Norway. Twenty-six of these (87%) were males. This is significantly greater than the expected 50:50 ratio found within the core areas ( $\chi^2 = 16.1$ , d.f. = 1, two-tailed  $P = 0.0002$ ). Age was determined for 24 of these males; 71% were 2- to 4-years old. This

is also significantly different from the expected 24%, based on the males killed in core areas in Sweden ( $\chi^2 = 28.9$ , d.f. = 1, two-tailed  $P < 0.0001$ ).

## Discussion

By using a 90% harmonic mean area, based on kill locations of females, to define core areas, it was ensured that about 90% of the females occurred within the core areas and that the relative density declined from the centre towards the edge. To avoid circularity, the tests in the present study were based on comparing locations and ages of males, which were not used to define areas, with those of females.

This study concludes that the brown bear population in Sweden is below carrying capacity, based on two lines of evidence. First, no 'plateau' in relative density was observed at the centre of the core areas, suggesting that carrying capacity has been reached in few, if any, areas in Sweden. However, the study recognizes that density alone does not show when carrying capacity has been reached. Secondly, the population is growing rapidly;  $r = 0.13$  in a northern study area and  $r = 0.15$  in a southern study area, based on observed rates of reproduction and mortality of radio-marked bears (Sæther *et al.*, 1998).

### IS THERE EVIDENCE FOR PRESATURATION DISPERSAL IN FEMALE BROWN BEARS?

As expected from Prediction 1, the density of females declined more steeply from the centre of the core areas towards the edge than did the density of males. This suggests that more males than females dispersed from the core areas. This was supported by the test of Prediction 2; there was a preponderance of males in the periphery and the males were dominated by bears in the age of most active dispersal. Prediction 3, that females in the periphery should be closer, on average, to the edge of the core areas than males, was not supported. Males and females in the peripheral area showed no statistical difference in distance from the core area boundary. This strongly suggests that the females exhibited presaturation dispersal. Because this

**Table 2.** Age structure, in percentage, of brown bears shot within core and peripheral areas in Sweden and in Norway

Age group (years)	Females		Males		
	Sweden		Sweden	Norway	
	Core	Periphery	Core	Periphery	All
1	23	10	24	15	8
2–4	36	40	24	45	71
≥5	41	50	51	39	21
<i>n</i>	78	10	86	33	24

conclusion was reached by comparing the distribution of males to that of females, it cannot be determined whether or not males showed presaturation dispersal, although it is thought to be occurring. It is important to stress that during the population bottleneck around 1930, there were only about 130 bears left in the small and isolated populations that subsequently survived in Sweden (Swenson *et al.* 1995). Thus, bears had been exterminated from today's peripheral area and most of today's core areas (Swenson *et al.* 1995), which means that females are in the peripheral area because of dispersal from the core areas. That bears did not previously occur in the present peripheral areas is thus more a reflection of history than of habitat differences.

This is, to the authors' knowledge, the first published evidence of presaturation dispersal in bears. Unfortunately, presaturation dispersal has been defined both as dispersal occurring when population growth rates are positive, and dispersal from a place of residency before the carrying capacity has been reached (Stenseth & Lidicker 1992). The former definition came from observations of dispersal in cyclic rodents (Krebs *et al.* 1973), whereas the latter is actually dispersal that is negatively density dependent. It is important to clarify that evidence of presaturation dispersal was observed by this study in a population that is growing rapidly (Sæther *et al.*, 1998).

The North American studies of bear dispersal referred to in the introduction were populations that were stable or declining; for example, Reynolds (1993) followed 32 subadult female brown bears in a population in Alaska that was declining as a result of overharvest. None of these females emigrated, i.e. moved beyond the mother's home range or immediately adjacent to it. The finding by the present study of females occurring in all zones up to 50–60 km from the core area and even up to 70–80 km in Sweden indicates much greater dispersal distances than Reynolds (1993) reported. As stated earlier, the home range diameter for an adult female brown bear in Sweden is about 24 km. There are also indications of presaturation dispersal when population growth is positive in other European brown bear populations, but not from low-density populations that are not increasing. The population in the northern part of European Russia increased dramatically from the early 1960s to late 1980s (Chestin *et al.* 1992) and a substantial net immigration to adjacent Finland was recorded by Pulliainen (1983) during his study covering the period from 1968 to 1982. In the Ukraine, the population increased rapidly from the mid-1950s to 1980, and bears recolonized all forested areas of the Carpathian Mountains in the country (Slobodyan 1993). The population in the core area in southern Slovenia has increased and bears have recolonized northern Slovenia and even farther, into parts of Austria and Italy (Adamič 1996). In contrast, no similar dispersal and recolonization has been reported from the three small, isolated and stable or declining populations in central

Italy and northern Spain (Zunino & Herrero 1972; Clevenger & Puroy 1991; Naves & Palomero 1993).

The evidence of presaturation dispersal is important for anticipating the future geographical increase, because the presence of even a few rapidly dispersing individuals can markedly increase the rate of spread in a population (Goldwasser, Cook & Silverman 1994). In addition, species showing presaturation dispersal may be more successful in coping with fragmented habitats (Lidicker & Koenig 1996). The increased dispersal rates are positive for gene flow among bears in different areas (Craighead & Vyse 1996) and for the survival of metapopulations (Hansson 1991). Because this dispersal appears to be manifested at positive population growth rates, removing limiting factors to obtain a positive growth rate may yield more positive results for bear conservation than just the positive growth rate itself. However, after bears have disappeared from an area, farmers can attend to their livestock less. Considerable losses to livestock, especially sheep, can occur when bears recolonize areas with free-ranging sheep (Adamič 1996; Sagør, Swenson & Røskaft 1997).

Data from the present study support Hartman's (1995) suggestion that dispersal patterns differ between populations that are continuous and those that are at the edge of an expanding population. This means that it is not appropriate to extrapolate results on dispersal behaviour from studies of continuous, nongrowing populations to expanding populations. Presaturation dispersal apparently occurs in several large mammal species from several taxonomic groups, although it was not found in another large carnivore, the lion (*Panthera leo* L.) (Hanby & Bygott 1987). Of the studies reporting presaturation dispersal in large mammals, listed in the introduction, only two specifically stated that the low-density populations that showed greater dispersal were increasing: Cheeseman *et al.* (1988) for badgers and Wahlström & Liberg (1995) for roe deer. In the future, researchers should report the population trend along with dispersal results. Hopefully, this should allow determination of the generality of presaturation dispersal in increasing large mammal populations.

#### STRUCTURE OF THE EXPANSION FRONT

As expected, the cross-section of the expansion front showed both a steep and a flat component. The relative density was halved every 20–30 km from the centre towards the edge of the core area. The observed sex ratio of hunter-killed bears was even within the core area. Because males are generally more vulnerable to hunting than females (Bunnell & Tait 1981), this probably means that females outnumbered males within the core areas. This is supported by the observation that the relative density of females declined more rapidly from the centre of the core areas towards the edge than did the relative density of males.

Results of the study reported here were based on bears harvested over a 13-year period. It would, of course, have been better if this period had been shorter. However, the slow rate of data accumulation in studies of bears precludes using short time periods. However, the wave front (Fig. 2) probably would have appeared steeper if data from a shorter period had been used.

Bear populations are notoriously difficult to census (Eberhardt & Knight 1996). Results of the present study suggest that it may be easier to extrapolate census results from study sites within peripheral areas to other peripheral areas, than from study sites within core areas to other areas within core areas, especially near the expansion front. The apparently large differences in density over short distances within the core area would complicate any effort to estimate population size near an expansion front.

#### THE STATUS OF BROWN BEARS IN NORWAY

This study showed clearly that the characteristics of the brown bears killed in Norway fit those of bears in a peripheral area; the sex ratio was heavily skewed towards males, and the males were primarily 2- to 4-years old. This strongly supports the conclusions of Elgmork (1988) and Swenson *et al.* (1995). The results refute the conclusion of Kolstad *et al.* (1986) that prior to 1982 the brown bear in Norway was found in healthy, reproducing populations. It should be mentioned that reproducing brown bears do occur in a small area of Norway between Finland and Russia (Swenson & Wikan 1996). It is recommended that the sex and age of killed bears be used in other areas where bear populations are expanding in distribution to identify core and peripheral areas.

#### Acknowledgements

We thank Jonas Kindberg for help with the GIS work. This study was supported by the Swedish Hunters' Association, the Norwegian Institute for Nature Research, the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, WWF-Sweden and Olle och Signhild Engkvists Stiftelser. We appreciate the helpful comments that Harry Reynolds, François Messier, Göran Hartman, John Linnell, Jonas Lemel and Kjell Wahlström gave us on earlier drafts of this paper.

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Received 24 April 1998; revision received 3 February 1998