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Changes in the structure of an increasing brown bear population with distance from core areas: another example of presaturation female dispersal?

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In stable and declining brown bear (*Ursus arctos*) populations, female dispersal is uncommon and female dispersal distances are short while in increasing populations the distance is not necessarily dependent on sex. The number of brown bears has strongly increased in Finland during recent decades, and the species has recently colonized the central and southern parts of the country. We examined changes in the sex ratio of hunter-killed bears and, from observational data, the proportion of cubs, litter size and proportion of cubs and litter size and proportion of adult males with distance from the Finnish-Russian border. Our results provided evidence that indicated the presence of male-biased dispersal, while no sex difference was noted in dispersal distance, thereby supporting the hypothesis of presaturation female dispersal in an expanding bear population. Small litters in the most peripheral area may result from recent dispersal by females that had not yet attained prime breeding age in the new area.

1. Introduction

Males are the predominant dispersing sex in polygynous mammals (Greenwood 1980, Usher 1986, Hartman 1995) such as brown bear (*Ursus arctos*) (Blanchart & Knight 1991, Mace & Waller 1997, Swenson *et al.* 1998). In stable and declining brown bear and black bear (*U. americanus*) populations, males usually disperse over considerable distances while females establish their home range close to or in their mother's home range (Rogers 1987, Blanchart & Knight 1991, Reynolds 1993). Swenson *et al.* (1998) were the first to demonstrate that in an increasing brown bear population that is expanding its geographical range, presaturation dispersal by subadult fe-

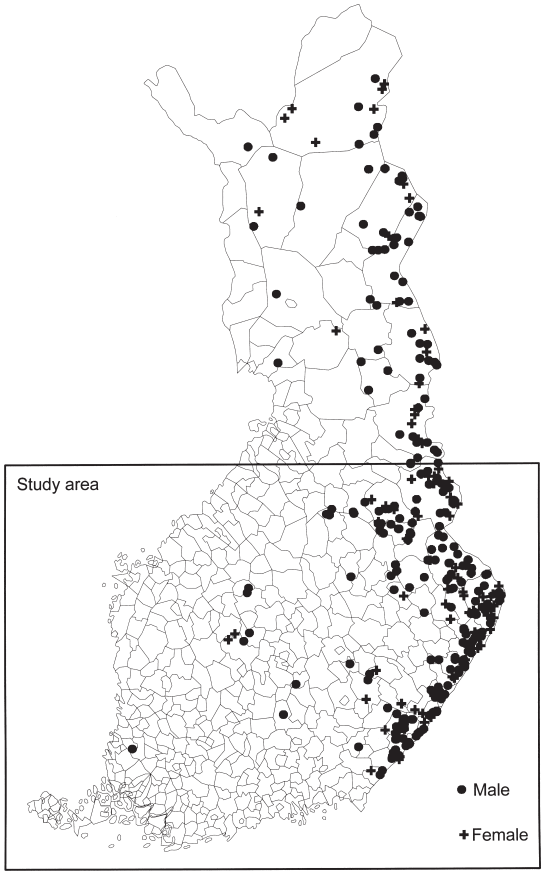

Fig. 1. Study area and location of brown bear kill sites in Finland in 1993–1998.

males can extend as far from their natal home ranges as that of subadult males.

After the major decline in numbers and distribution that occurred in the late 19th century (Palmen 1913), the brown bear population range in Finland was restricted purely to the northern and easternmost parts of the country up to the 1970s, during which the species initiated gradual expansion of its range to the west and south (Pulliainen 1990). Since the late 1960s, brown bear numbers have shown a roughly 5-fold increase, and the animal is currently also inhabiting the western and southern parts of Finland (Pulliainen 1997). It is not possible to time the first litters observed outside easternmost Finland exactly, but the very first were seen in central Finland during the late 1980s and in western and southern Finland in the early 1990s (oral communication by authors with the staff of local Game Management Districts).

North western Russia is inhabited by a dense, stable brown bear population (Danilov *et al.* 1998, Danilov 1999). We investigated how the predicted male-biased dispersal is associated with the sex ratio of hunter-killed bears and the relative proportion of cubs and adult males in zones at varying distances from the Finnish-Russian border. Brown bears disperse most actively as subadults 2–4 years of age (Swenson *et al.* 1998). Since litters born to first-breeders are smaller than those born to prime breeding age females (Sellers & Aumiller 1994), we also examined the association between distance from the border and litter size.

2. Material and methods

The study area was located in southern part of Finland (Fig. 1), west of a high-density bear population (*see* Danilov 1999). In the easternmost zone of this part of the country, bear densities are much higher than elsewhere in Finland (Nyholm 1995), and emigration from Russia and expansion from eastern to western Finland has been most active within this section (Pulliainen 1997). We analysed predicted shifts in the sex ratio of hunter-killed bears with distance from the Finnish-Russian border by establishing 5 zones so that at least 30 bears were included in each zone. The kills were strongly concentrated close to the border (Fig. 1) and the resultant zones were therefore 0–10, 11–20, 21–40, 41–80, and > 80 km from the border. The trend for decreasing proportions of females in the zones was analysed by comparing the sex ratios of bears killed within the zones.

Observational data collected by local experts during 1996–1998 comprised 11 559 brown bear observations. We counted the proportion of females with cubs (cubs-of-the-year and dependent yearlings) in all the observations and the proportion of adult male tracks (front pawprint wider than 14 cm) in the track observations within 8 distance zones. These zones were formed as follows: (1) we coded each observation with an individual identification number corresponding to a 50 × 50-km square and measured the distance of the midpoint of each square from the borderline and (2) we formed the following zones from these distances: 0–49 (1), 50–99 (2), 100–149 (3),

150–199 (4), 200–249 (5), 250–299 (6), 300–349 (7) and > 349 km (8). If the midpoint of the square was located in Russia, the square was designated as belonging to the first zone. The patterns of change across distance zones were tested with Spearman's rank correlation analysis.

In analysis for litter size we focused on litters-of-the-year, because the age at weaning may vary regionally. The data were from 1997 to 1998, before which the observers were advised to measure the cub tracks so that the cubs-of-the-year could be distinguished from yearling cubs. The observation was designated as a litter-of-the-year when the width of the front pawprint did not exceed 5 cm in April–May, 6 cm in June, 7 cm in July and 8 cm in August–November. These upper limits are based on the authors' personal experience. Each accepted observation was placed on the map and other observations were removed when the number of cubs was similar within radius of 25 km, suggesting 491 km^2 as a theoretical home range for litters-of-the year. This assumption is safe because the mean annual home range of a female bear is 345 km^2 in Scandinavia and females with cubs move within areas smaller than this average (Swenson *et al.* 1999). The distance from each litter to the eastern border was measured, and the differences between litters of varying size were analysed with the Kruskal-Wallis test.

Except for comparison of sex the ratio of bears shot in the eastern border area and in core areas of Scandinavian bear populations, all the reported probabilities p are 1-tailed, because the directions of the differences expected were based on published literature.

3. Results and discussion

The sex ratio of hunter-killed bears was male-biased even in the eastern border area (Table 1), and the proportion of males among bears shot 0–10 km from the border was significantly higher than in core areas of the Scandinavian bear population where 49.3% of hunter-killed bears were males (n = 393, χ^2 for difference = 11.2, df = 1, p = 0.001; cf. Swenson *et al.* 1998: 822). The sex ratio did not differ from that of bears shot in the peripheral area in Norway (χ^2 = 0.7, df = 1, p = 0.401; cf. Swenson *et al.* 1998: 822). Since the sex ratio of hunter-killed bears was strongly male-biased even in the eastern border area, we could not designate even these areas as core regions. In Sweden, females followed by either cubs or yearlings are protected from hunting, while in Finland only females followed by young-of-the-year are protected. Despite clear differences between sex ratios of bears shot in the Scandinavian core regions and in Finland, it is premature to conclude whether Finland belongs entirely to the western periphery of the Eastern European brown bear population before actual hunting practices have been investigated. In Russian Karelia, where females with cubs-of-the-year are protected as in Finland, about 70% of hunter-killed bears are males (P. Danilov, unpubl. data). Baiting is prohibited in Finland, while allowed both in Sweden and Karelia. Therefore, the difference in sex ratio of bears shot in the core areas in Scandinavia and Russian Karelia is surprisingly clear and unexplainable so far.

No trend in sex ratio was discernible across the distance zones (Table 1) and the sex ratios of bears killed within the different distance zones did not differ from each other (χ^2 = 4.2, df = 4, p = 0.385). This result provided evidence for similar dispersal distances of males and females, as reported by Swenson *et al.* (1998) for expanding Scandinavian bear populations.

Brown bears disperse most actively as subadults at 2–4 years of age (Swenson *et al.* 1998). Our sample of bears assessed for age was so small (n = 120) that we could not properly analyse for differences in the relative proportion of different age-classes within the various zones. In pooled data on the sexes, a trend towards an increasing

Table 1. Subadult and adult brown bears shot at different distances from the Finnish-Russian border in Finland.

Distance (km)	Subadults (2–4 years old)	Adults (> 4 years old)
0–10	22	23
11–20	12	12
21–40	12	9
41–80	7	2
> 80	14	7

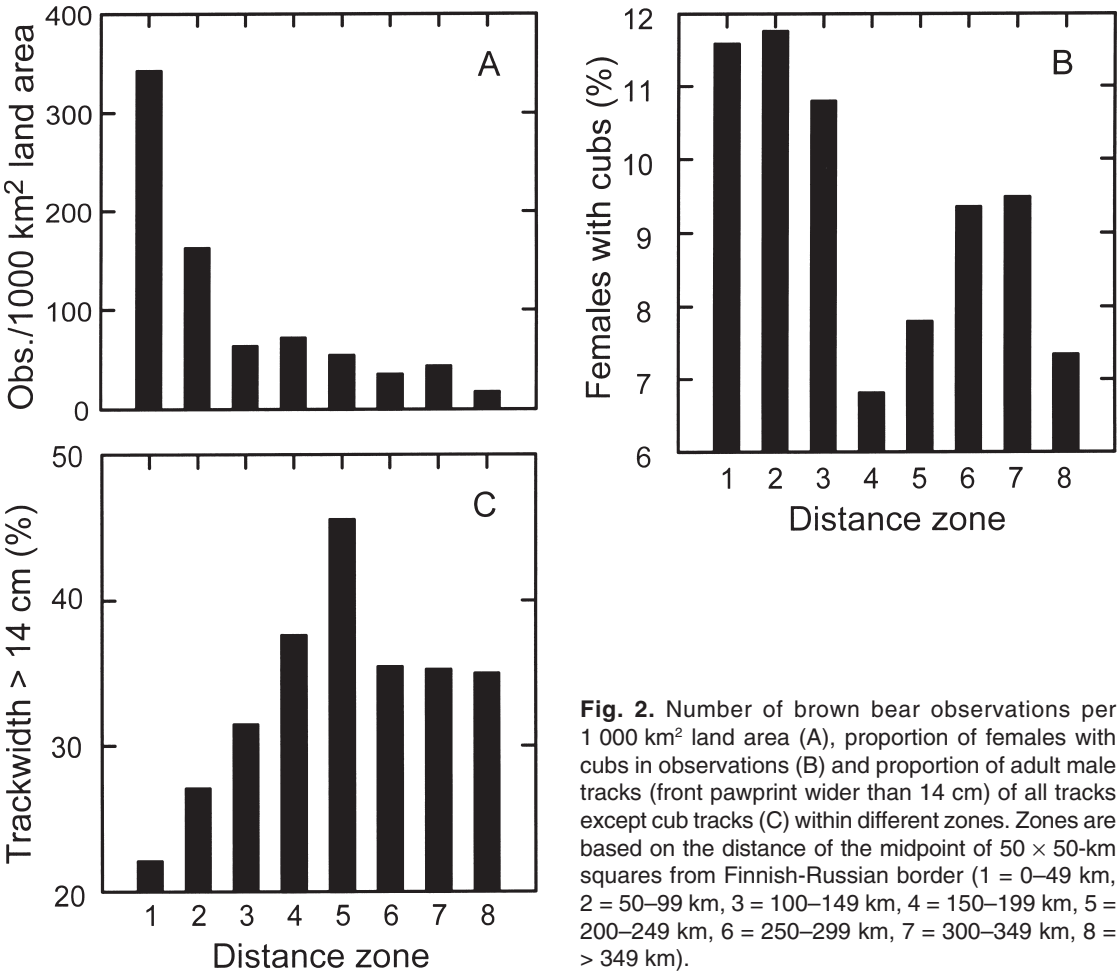

Fig. 2. Number of brown bear observations per 1 000 km^2 land area (A), proportion of females with cubs in observations (B) and proportion of adult male tracks (front pawprint wider than 14 cm) of all tracks except cub tracks (C) within different zones. Zones are based on the distance of the midpoint of 50 × 50-km squares from Finnish-Russian border (1 = 0–49 km, 2 = 50–99 km, 3 = 100–149 km, 4 = 150–199 km, 5 = 200–249 km, 6 = 250–299 km, 7 = 300–349 km, 8 = > 349 km).

proportion of subadults occurs with increasing distance (Table 2). It is noteworthy that the Finnish practice of allocating hunting licences provincially on the basis of population estimates for the province does not allow proper analysis of differences.

Table 2. Proportion of male bears older than 2 years of age shot in Finland at different distances from the Finnish-Russian border in Finland.

Distance (km)	Males (%)	*N*
0–10	69.4	85
11–20	72.3	47
21–40	57.1	49
41–80	74.2	31
> 80	73.5	34

The number of bear observations per land area provided evidence of a drastic decline in bear density with distance from the Finnish-Russian border (Fig. 2A). The highest proportions of cubs were observed within zones 0–149 km from the border (Fig. 2B), and the proportion was correlated negatively with the distance (r_s = –0.643, p = 0.05, n = 8 distance zones), which indicated male-biased dispersal from the east. The mean number of cubs observed per litter was highest within zones where the proportion of females with cubs was highest (r_s = 1.00, $p < 0.001$, n = 8 distance zones), which may be due to the age distribution of females. In areas most recently colonized by females, smaller proportions of the females may be old enough to produce large litters (cf. Sellers & Aumiller 1994). No differences in food resources that could potentially affect litter

size (Strigham 1983) were evident between eastern and western Finland. The distance from the border was associated with the litter size (Kruskall-Wallis test statistic = 7.4, $p = 0.025$), being shortest for litters of 3 or 4 cubs and greatest for litters of 1 cub (Fig. 3). The long dispersal distance of females was evidenced by the location of some confirmed litters up to 300–400 km from the border (Fig. 2).

The proportion of adult male tracks (front pawprint wider than 14 cm) in track observations increased linearly across the first 5 zones, while stabilizing at lower levels at distances greater than 250 km from the border (Fig. 2C). The lower proportion in most peripheral regions may be due to a higher proportion of subadult males. The pattern could either be connected with earlier colonization by males of zones between 150 and 250 km or shorter dispersal distances by adult than subadult males. Although dispersing males are usually subadults, adult male dispersal may also be common, e.g. in Poland, adult males outnumber younger bears among emigrants from the east (Gula & Krakowiak 1996). These adult males may have possibly had lower-than-average mating success in areas of high bear density.

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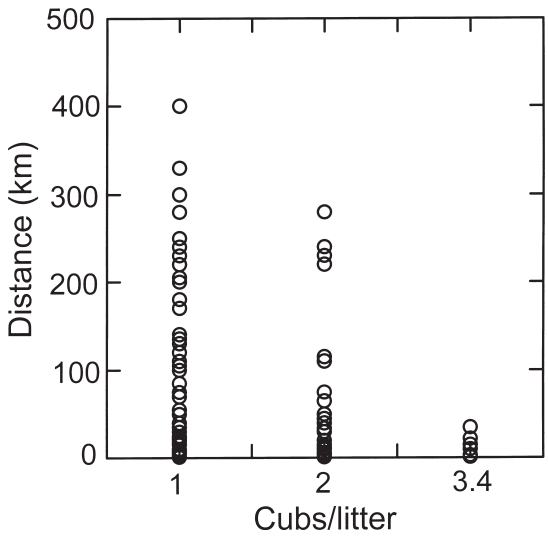

Fig. 3. Relationship between brown bear litter size in Finland and distance from the Finnish-Russian border.

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