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The structure of the expanded brown bear population at the edge of the Finnish range

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Based on the geographic location of male and female bears shot in Finland in 1954–2003, we examined regional differences in the population structure of peripheral brown bear (*Ursus arctos*). More bears were shot in western and northern locations in 1954–1963 than in 1993–1998. Between 1954–1963 male and female bears were shot in equal proportions, whereas between 1993–2003 more males than females were shot in western and northern locations. During 1968–1995, the population growth rate was strikingly higher in southern than in northern parts of Finland. Our results provide evidence that the peripheral Finnish brown bear population increases towards both the north and west, which may occur because of a higher harvesting rate in the north and a recent population expansion from the east.

Introduction

A range expansion in animal populations is influenced by factors that affect dispersal and population growth (Wielgus & Bunnell 1994, Swenson *et al*. 1998, Ims & Hjermann 2001). In brown bear (*Ursus arctos*), females are significantly more philopatric than males (Blanchart & Knight 1991, Mace & Waller 1997, Swenson *et al*. 1998, McLellan & Hovey 2001) and long-distance female dispersal has been documented only within populations at presaturation densities (Swenson *et al*. 1998).

The Finnish brown bear population may represent an example of a peripheral population, because a part of the western edge of the Eurasian distribution zone was recently located in eastern Finland (Pulliainen 1990). Due to the population increase and expansion during the last few decades (Nyholm 1990, Pulliainen 1990, 1997), bears are observed throughout the country. The proportion of males and subadult bears, however, increases with the distance from the eastern core areas (Kojola *et al*. 2003). Previous studies of the Finnish bear population structure (Kojola & Laitala 2000, Kojola *et al*. 2003) did not consider sex and age effects simultaneously, nor were the factors relating to the South–North direction explored.

We examined long-term spatial changes in brown bear population and population structure in Finland in light of predictions derived from female-biased philopatric behavior. Because dispersal tendencies are highest among subadult males (Swenson *et al*. 1998), we predicted, due to the recent recolonization from the east (Pulliainen 1983a, 1983b, 1997), that the proportion of subadult males will increase towards the west. We also examined the change in population structure along the South–North gradient because population density in northern Finland is much lower than that in southern Finland (Kojola 2002).

Material and methods

Finland was divided into the northern and southern segments, with the northern area comprising the reindeer management area and the southern part represented by the rest of Finland (Fig. 1). We calculated population annual growth rate (λ) between 1968 and 1995 separately for the northern and southern areas using the formula EXP $([\ln(E_{t1}) - \ln(E_t)]/(t_1 - t))$ in which E is the population estimate, t_1 equals year 1995 and t equals year 1968. To achieve 1968 population estimates for the different parts of the country, we divided the countrywide estimate (150; Pulliainen 1983a) according to the proportions of bears shot in Finland in 1966–1969 in these areas (75.9% in the northern area, n = 278, cf. Mäensyrjä 1971). As such, we assume 110 bears for the northern area and 40 bears for the southern area. Estimates for 1995 (170 in the northern area and 560 in the southern area) were published by Anonymous (1996). The number of Finnish–Russian border crossings by bears was 5-fold higher in 1995 than in 1968 (Pulliainen 1997), which is in accordance with the difference in population estimates (150 *vs*. 730).

Data on the locations of female and male bears shot in Finland (Fig. 2) in 1954–1963 were extracted from a map published by Pulliainen (1963). In 1993–2003 hunters used forms and maps for recording information about killed bears. Most bears (81.0%) shot in 1996–2003 in southern Finland (n = 695) were aged based on cementum annuli in rudimentary premolar teeth (analysed at Matson's laboratory, Montana). Unfortunately, we were able to collect premolar data from less than half of the hunter-killed bears (39.2%) in northern Finland (n = 148).

We compared the geographic location of bears shot in the northern area in 1954–1963 and 1993–1998. The more recent period was limited to years prior to 1999, because in the beginning of 1998 the reindeer management area was subdivided into western and eastern hunting areas, each with separate quotas. We compared the sex ratio of bears shot in northern and southern Finland and the location of males and females in the entire study area in 1993–2003. To evaluate the effect of age on home-range location, we divided the aged bears into subadults (2–4 years of age) and adults (> 4 years of age).

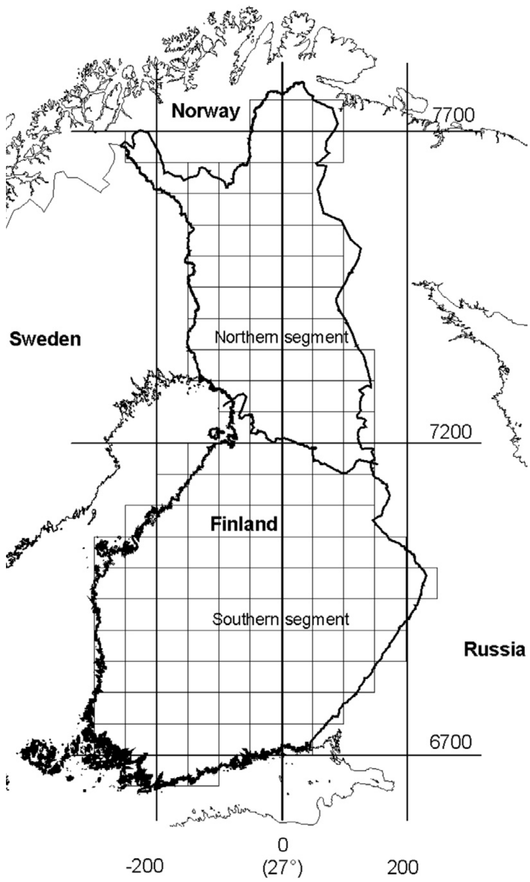

Fig. 1. The two study areas and distances from equator and 27° meridian (km).

We used two parameters for the location of each bear. In the South–North direction, the location was the distance from the equator (km), and in the West–East direction the distance from the 27° meridian (Fig. 1). Because the distances did not meet the assumption of normality (Lilliefors probabilities < 0.05 in Kolmogorov-Smirnov test) we used Mann-Whitney U-test when one independent variable was available. When two independent variables were treated simultaneously (sex and age class for year period 1993–2003) we sorted cases by distance and

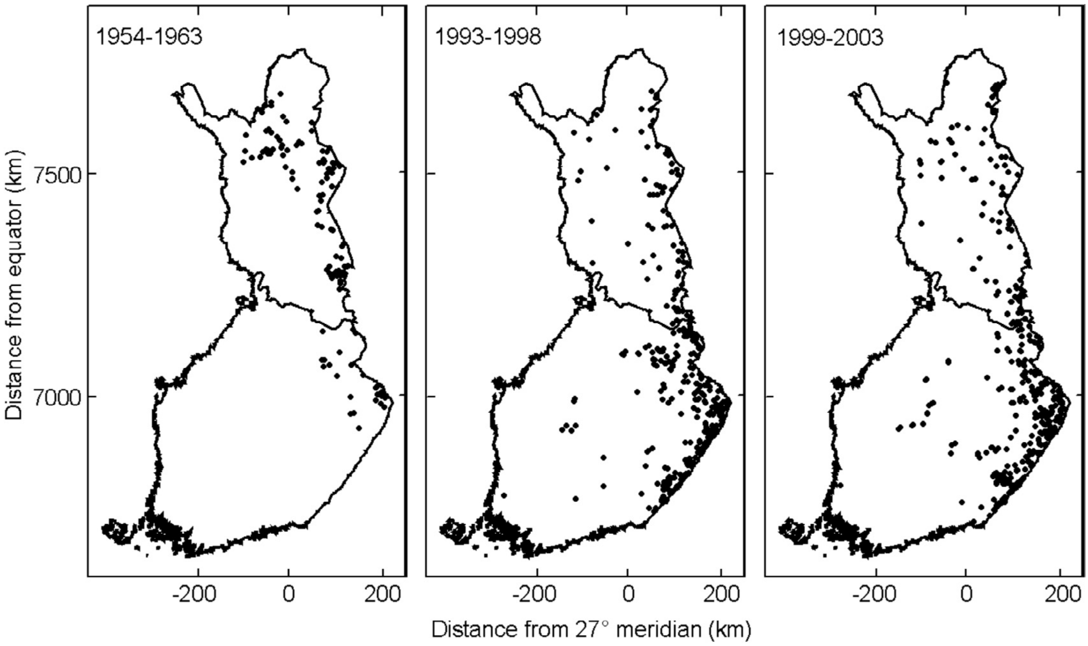

Fig. 2. Locations of bears shot in Finland during (data for 1954–1963 from Pulliainen 1963).

then recovered the distances with rank orders which enabled us to perform parametric tests (two-way ANOVAs; Conover & Iman 1981).

Results and discussion

Bears shot between 1954 and 1963 were located in more western and northern locations than were the bears shot between 1993 and 1998 (Fig. 3, Mann-Whitney *U*-test: $U_{120,802}$ = 65473, P < 0.001, U = 15216, P < 0.001, respectively). This difference between the eastern and western locations remained when the comparison was made for the northern study area only ($U_{94,83}$ = 2991, P = 0.007, U = 4941, P = 0.002, respectively, Fig. 1). These data suggest that the edge of the northern section core area was located more western and northern in 1954–1963 than in 1993–1998. Harvest rates in the northern area during the 1960s were evidently very high, because the official statistics indicate that the mean number of bears shot annually between 1963 and 1968 was about 3 times higher than that between 1993 and 1998 (Mäensyrjä 1971, Kojola *et al.* 2004). For example, in 1968 when the population estimate for the whole country was 150 bears (Pulliainen 1983a), 51 bears were harvested in the northern segment (Mäensyrjä 1971). The harvest rate was far above the estimates for sustainable harvest in brown bear populations (Knight & Eberhardt 1985, Miller 1990, Swenson *et al.* 1994).

Between 1993 and 2003, the average location across the West–East gradient was associated with the bear sex (ANOVA: F = 7.90, df = 1,311, P = 0.005, Fig. 4), but not with age (F = 0.41, P = 0.525). There was no two-tailed interaction detected between sex and age on location (F = 1.27, P = 0.260). Males were also shot in more northern locations than females (F = 12.03, P = 0.001). There was no age effect and no two-tailed interaction effect between age class and sex on location in the South–North direction (age effect; F = 0.37, P = 0.543, interaction; F = 0.21, P = 0.647). The sex ratio was more male-biased in the northern area (73.9%, n = 184) than in the southern area (64.2%, n = 618, χ^2 = 5.92, df = 1, P = 0.015). The sex ratio did not differ with the location in either the West–East direction or the south-north direction in 1954–1963 (Mann-Whitney *U*-test: $U_{87,33}$ = 1493, P = 0.735, U = 1439, P = 0.984).

The annual growth rate (λ) of brown bear populations in 1968–1995 was lower in northern

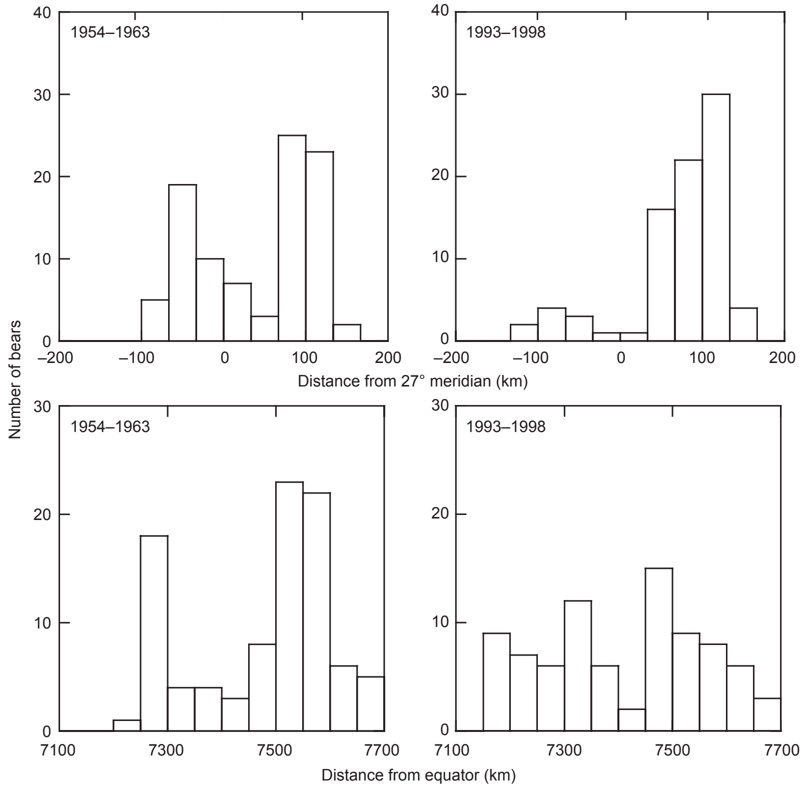

Fig. 3. The distribution of the location of the hunter-killed bears in South–North and West–East directions (data for 1954–1963 from Pulliainen 1963).

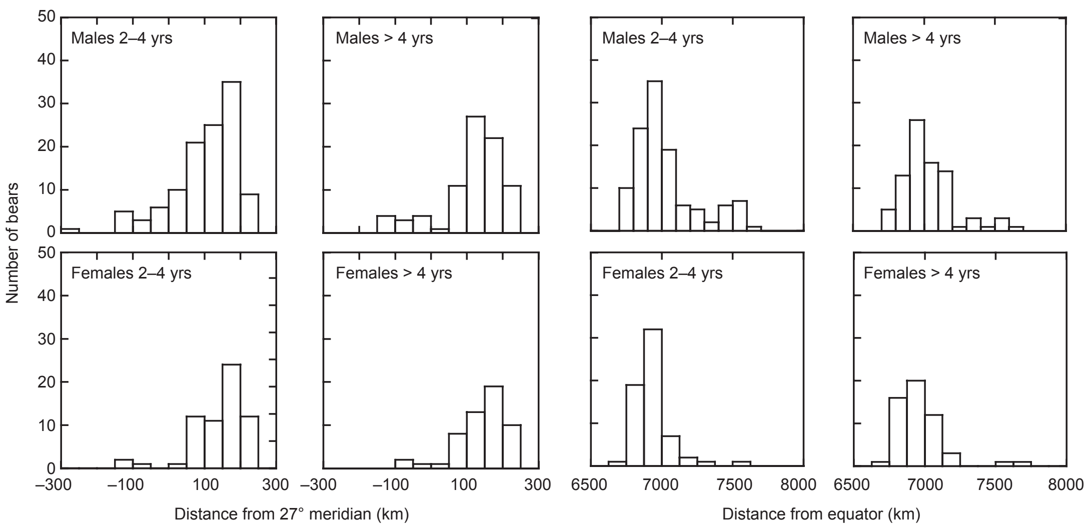

Fig. 4. The distribution of the locations in South–North and West–East direction, shot in 1993–2003 in Finland.

than southern Finland (1.016 and 1.103, respectively). Estimates of harvesting rates are lacking, but the 6-fold lower population growth rate in the northern study area may be due to a higher harvesting rate, because human harvest is usually the only important mortality factor in low-density brown bear populations (Servheen 1990). The differences in harvesting rates between northern and southern Finland likely result from differences in management policy. For example, in the early 1970s, bears were protected in many southern localities while no protection existed in the northern areas (Mäensyrjä 1971).

Although we predicted that the proportion of subadult males would increase from east to west, the results of our ANOVA model with rank-transformed locations did not support this prediction. The more western location of males (Fig. 4), however, was in line with the hypothesized peripheral nature of the Finnish bear population as it increases with the distance from the eastern core regions (Pulliainen 1983, 1997, Kojola & Laitala 2000, Kojola *et al*. 2003). Our results also indicate that the bear population in northern Finland remained more peripheral than in southern Finland.

The results of this study indicate a link between expansion history and regional differences in adult sex ratio in a species that has a sex bias in dispersal, and also suggests a connection between harvest rate and sex ratio. These findings are relevant for the future management and harvest policy, because population growth rate is likely to be correlated with the proportion of adult females in the population.

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