Regional differences in density-dependent mortality and reproduction in Finnish reindeer

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Abstract: Reindeer in the southern and central regions of reindeer husbandry in Finland feed on arboreal lichens or are given supplementary rations from midwinter whereas in the northern region reindeer use snow-covered forage throughout winter. Rates of mortality and reproduction were examined using data from population crashes of semi-domesticated reindeer that occurred in Northern Finland during 1960–1987. The mortality and reproductive rate were density-dependent in the southern region and the mortality was density-dependent in the central region. The density-dependence was most probably due to food competition in forest cutting areas where reindeer gather to feed on arboreal lichens from felled trees. In the northern region mortality was not density-dependent indicating that where reindeer feed on over-utilized winter range the effects of increased feeding competition are masked by very large changes in the availability of forage.

Key words: Density-dependence, mortality, reproduction, forest cutting, reindeer, Finland

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Introduction

The fecundity of females and the survival of juveniles are susceptible to food limitation regulation in many ungulates (Eisenberg, 1981; Sauer and Boyce, 1983; Clutton-Brock *et al.*, 1987). In wild reindeer, density-dependent food limitation restricts population size above all through calf mortality (Skogland, 1985; 1990). Andreev (1971) suspected that density-dependent effects might occur in populations of semi-domesticated reindeer but none have been reported.

The number of semi-domesticated reindeer in Finland fluctuated considerably during the 1960s and 1970s owing to heavy natural mortality (Helle and Kojola, 1993). Numbers have now recovered and the density of reindeer has doubled yet there have been no large-scale crashes. This is a result of new management practices, which include slaughtering calves and providing supplementary feed in winter (Helle and Kojola, 1993; Kojola and Helle, 1993).

The aim of this study was to assess density-dependent natural mortality and the reproduction in different reindeer husbandry regions in Finland. The winter feeding habits of reindeer show a regional pattern. In the northern region, reindeer use snow-covered foods throughout the winter, while in the southern regions they feed on arboreal lichens in midwinter (Helle and Saastamoinen, 1979). Since the mid

1970s the reduced availability of arboreal lichens caused by large-scale logging and air pollution (Helle *et al.*, 1990b) has been compensated for by supplementary feeding. Regional differences in the effects of density on mortality and the reproductive rate may be expected as a result of these differences in winter feeding ecology. Reindeer that feed off the ground compete for the best feeding sites and dominant individuals commonly take over snow craters dug by subordinates. The interaction frequency increases during the course of the winter (Helle, 1984; Skogland 1989). Reindeer that feed on arboreal lichens are usually much more scattered and interact less frequently. In late winter, therefore, the food intake of individual reindeer is less likely to be influenced by competition compared with reindeer in the north. Consequently, mortality and reproduction might be expected to be more density-dependent in the north than in the south.

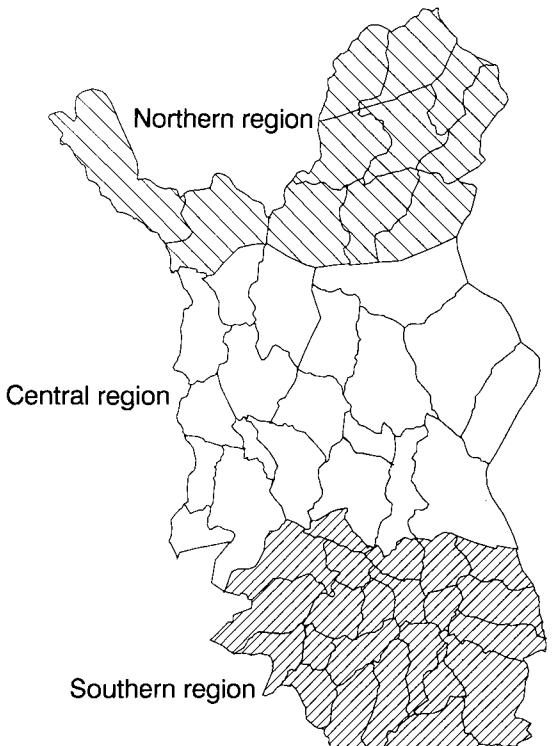

Fig. 1. Reindeer management area of Finland, showing the regions used in this study. The period of digging for food from beneath the snow; northern herds: 7 months; central herds: 5 months; and southern herds: 3 months.

Study area and methods

The reindeer management area of Finland is divided into 56 herding associations, varying from 558 to 5580 km^2. The herds were combined into 3 regions (Fig. 1), according to the length of the period in winter during which reindeer dig for food from beneath the snow. This period is ca. 7 months in the northern region (n = 11 herds), 5 months in the central region of the management area (n = 21 herds) and ca. 3 months in the southern region (n = 24 herds; Helle and Saastamoinen, 1979; Helle and Tarvainen, 1984).

The mean winter densities of reindeer among all herds varied in 1960–1973 from 0.11 to 2.56 and in 1974–1987 from 0.51 to 3.03 animals km^2 (Helle and Kojola, 1993). The overall density per land area was highest in the northern region, while the density per range suitable for terricolous lichens was highest in the southern region (Helle *et al.*, 1990). The maximum permitted stocking rate for a herding association was set every tenth year by the state authorities. These numbers have been largely based on proposals made by the herding association in question.

Data about the number of reindeer were obtained from the records kept by the Association of Reindeer Herders. The accuracy of counts is unknown but < 2 % of animals go unmarked and there is no difference in the proportion of unmarked animals between different areas (Autto, 1980; Niittyvuopio, 1981). Calves were counted in midsummer and culling took place in early winter. Natural mortality was calculated from the difference between the post-harvest number of reindeer and the preharvest count in the subsequent year (calves born between counts were excluded).

The relationship between mortality rate or calf/female ratio and reindeer density within each region was determined for each 28 years (1960 - 1987), using data from each separate herd. The analysis yielded 28 Pearson correlation coefficients for both mortality and calf/female ratio in each of 3 regions. The coefficients from different regions were compared within years using Kruskal-Wallis one-way tests. The variation in the relationship between these coefficients and the mean mortality rate between regions was investigated by calculating simple regression equations. All statistical pro-

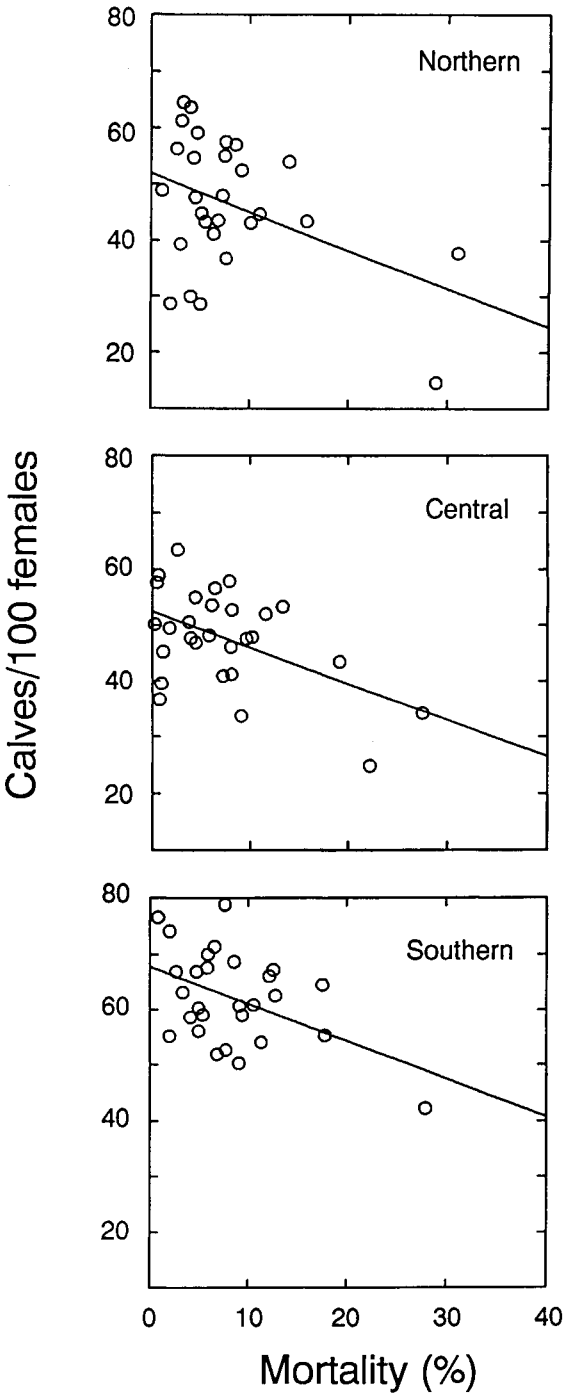

Fig. 2. Relationship between mean annual mortality and calf/female ratio in Finnish semi-domesticated reindeer during 1960–1987 (northern region: y = 51.934 - 0.688X, r = -0.412, n = 28, P = 0.029; central region: y = 52.474 - 0.650X, r = -0.499, n = 28, P = 0.007; southern region: y = 67.805 - 0.676X, r = -0.465, n = 28, P = 0.013).

cedures were performed by use of SYSTAT statistical software (Wilkinson, 1988).

Results

Correlation coefficients between natural mortality and population density did not vary among regions (ANOVA, H = 1.118, P = 0.572). The mean coefficient for the calf/female ratio decreased from north to south (all years combined, means 0.266, 0.063 and - 0.114, respectively, H = 20.949, P < 0.001). Annual mean of the calf/ female ratio was inversely related to the annual mean morality within each region (Fig. 2).

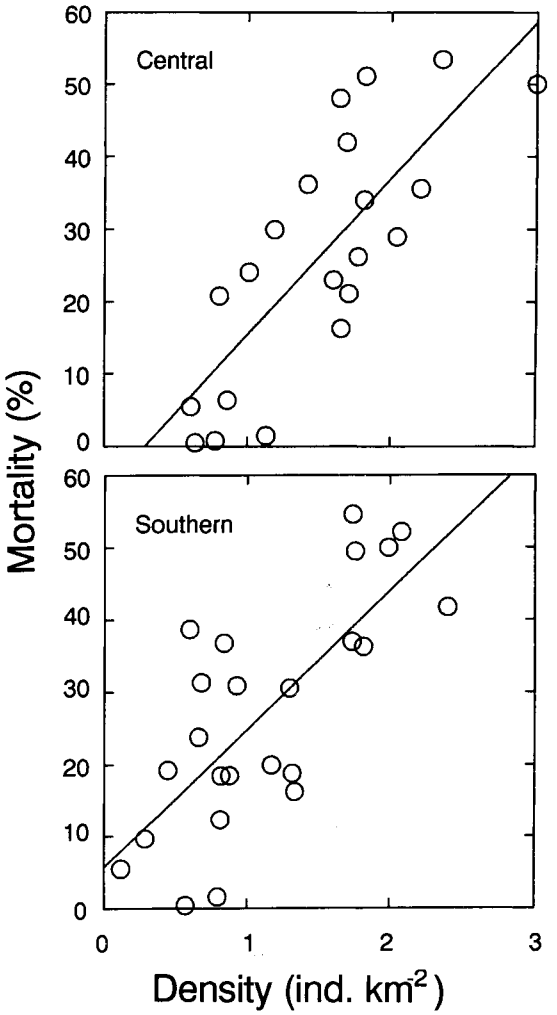

Fig. 3. Relationship between reindeer density and mortality of Finnish semi-domesticated reindeer in the central and southern regions in 1969 (central region: y = -6.069 + 21.544X, r = 0.780, n = 21, P < 0.001; southern region: y = 5.690 + 19.160X, r = 0.736, n = 24, P < 0.001).

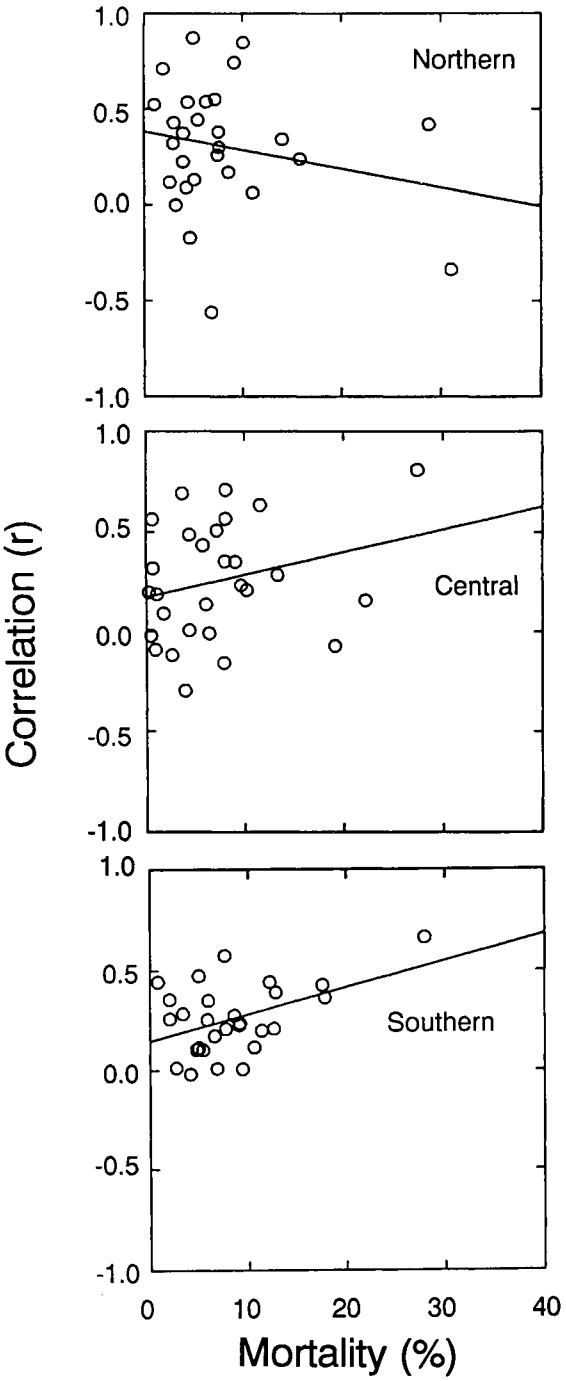

Fig. 4. Relationship between mean annual mortality and the correlation coefficient between density and mortality in Finnish semi-domesticated reindeer during 1960 - 1987 (northern region: y = 0.383 - 0.010X, r = -0.210, n = 28, P = 0.282; central region: y = 0.173 + 0.011X, r = 0.258, n = 28, P = 0.184, southern region: y = 0.147 + 0.013X, r = 0.445, n = 28, P = 0.018).

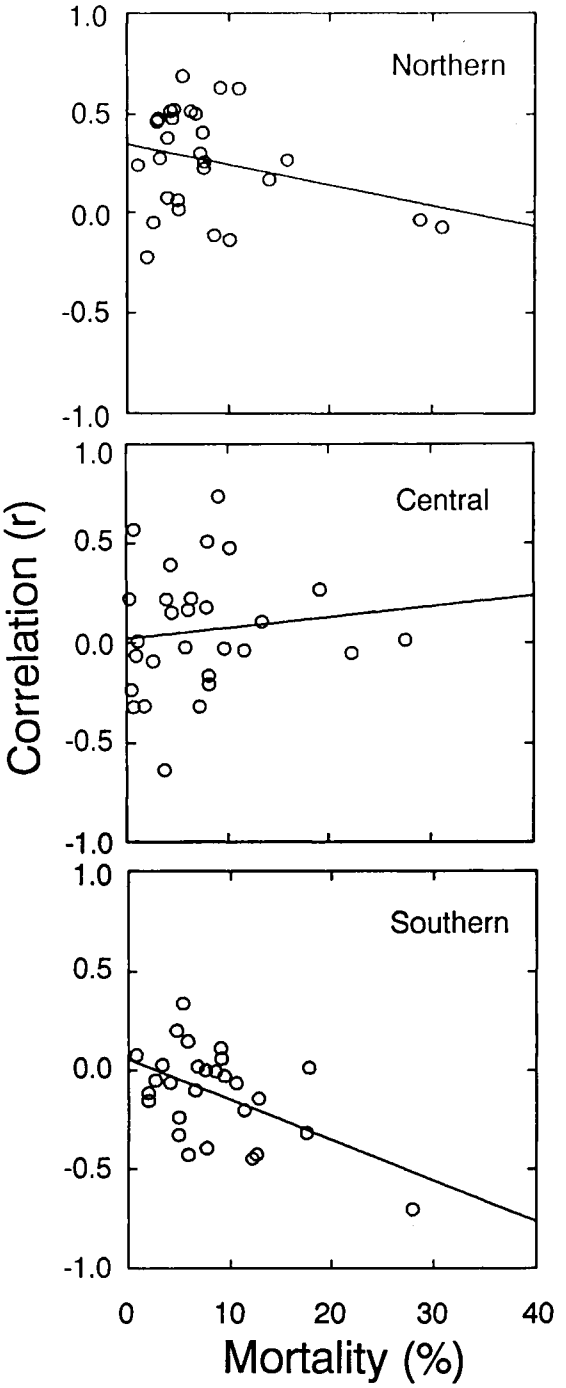

Fig. 5. Relationship between mean annual mortality and correlation coefficient between density and calf/female ratio in Finnish semi-domesticated reindeer during 1960 - 1987 (northern region: y = 0.350 - 0.010X, r = -0.280, n = 28, P = 0.144; central region: y = 0.023 + 0.005X, r = 0.117, n = 28, P = 0.311; southern region: y = 0.057 - 0.020X, r = - 0.515, n = 28, P = 0.005).

Mortality was most strongly density-dependent in the southern and central regions in 1969, when the largest population crash occurred (Fig. 3 and 4). The calf/female ratio was inversely density-dependent in the southern region in 1969 ($r = -0.072$, $n = 24$, $P < 0.001$).

The relationship between reindeer density and mortality rate was positively correlated with the mean mortality rate in the southern and central regions (Fig. 4). Moreover, the correlation between the calf/female ratio and population density was inversely related to the mean mortality rate in the southern region (Fig. 5).

Discussion

These results provide no evidence that the effects of density-dependent food limitation on mortality and reproduction are associated with use of snow-covered foods during winter. On the contrary, density-dependent changes in reproduction and natural mortality were detected only in the southern region where the period during which reindeer dig for food below the snow is shortest.

The lack of density-dependent mortality or reproduction in the northern herds might be due to large regional variation in the availability of forage caused by snow and ice. The information available about snow conditions associated with crashes in herd size indicates that the heaviest crashes occur when icing in early winter was followed by heavy snow accummulation (Helle, unpublished).

Reindeer that forage snow-covered food in woodland have to dig through deeper snow layer than those foraging on the wind-swept mountains. In the northern region, the reindeer densities are highest in herding associations located north of the timberline (Helle *et al.*, 1990). The biomass of the most preferred winter food, terricolous lichens (*Cladinia* spp.) is lower there than in herding associations located in the coniferous forest zone (Mattila, 1981), but the availability of the lichens is probably greater owing to thinner snow. Another possible explanation is based on the way in which herd size is manipulated (Helle and Kojola, 1993). The highest permitted stocking levels for reindeer are estimated independently in each herding association, and are based on the condition and behaviour of the animals. Culling reindeer in poor condition and stray individuals from another herding associations buffered the herds against the effects of density-dependent food-limitation by increasing the mean body weight of animals and reducing the increase in local population density.

Both the unexpected results - the close correlation between density and mortality in the southern and central regions and the correlation between density-dependence and the mean rate of mortality in the southern region - are most probably caused by the same factor: density-dependent food competition in forest cutting areas. Reindeer commonly gather to forage on arboreal lichens on felled trees, forming temporary aggregations of several hundred animals in a single cutting area (Rajala, 1967). Direct resources defence competition very likely occurs at these sites. The level of competition is likely to be a function both of the snow conditions and reindeer density. Therefore, we suggest that food competition on the lichens on felled trees explains this density-dependence. Unfortunately, this hypothesis cannot be tested because reindeer no longer gathering in forest cutting areas owing to the practice of providing supplementary feed.

The explanation presented here is associated with the question of whether or nor population dynamics and behaviour of semi-domesticated reindeer can be explained without considering human influence in the herds. One well-known misinterpretation is the seasonal migration of reindeer people between the sea coast and inland in northern Fennoscandia. This was originally considered to be an adaptation to the behaviour of the wild ancestors of semi-domesticated reindeer, but in reality the tradition has been initiatied by human interests (Tanner, 1929; Wiklund, 1948). No doubt intensive winter herding, assistance in opening up feeding craters by reindeer herders, felling trees rich in arboreal lichens and the motorization of herding routines have modified the behaviour of semi-domesticated reindeer.

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