Productivity of semi-domesticated reindeer in Finland

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Abstract: In spite of a twofold increase in the density of reindeer in Finland from 1974 to 1987, meat production per reindeer increased during this period. This was possible due to calf harvesting and supplemental feeding. Results from multiple regression models indicated that calf harvesting influenced both per unit area and per capita production more than supplemental feeding. Correlation between meat production and animal density decreased with increased supplemental feeding. Traditionally, southern and central herds of reindeer fed mainly on arboreal lichens in late winter; however, due to large-scale logging, woodlands rich of arboreal lichens had been greatly reduced. Economic carrying capacity of the winter range apparently has been exceeded in the south; a heavy crash in the number of reindeer is likely if supplemental feeding ceases. In northern herds, intensive calf harvesting enabled satisfactory yield without supplemental feeding. In northern herds, yield increased mainly per unit area (i.e. by increases in herd size); in the south yield per reindeer increased.

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Key words: reindeer, meat production, Finland, calf harvest, supplemental feeding

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Tiivistelmä: Huolimatta Suomessa vuosien 1974 ja 1987 välillä tapahtuneesta porotiheyden kaksinkertaistumisesta, lihantuotto poroa kohti kasvoi jakson aikana. Tämä johtui oletettavasti vasateurastuksesta ja lisäruokinnasta. Monimuuttujaregressiomallien tulosten perusteella vasateurastuksella näyttäisi olevan lisäruokintaa suurempi vaikutus sekä poroa että pinta-alaa kohti laskettuun tuottoon. Ruokinnan tehostuessa pienentyi lihantuoton ja porotiheyden välinen riippuvuus. Eteläosan ja keskiosan porot syövät perinteisesti puussa kasvavia jäkäliä kevättalvella. Hakkuista johtuen luppometsien osuus on suuresti vähentynyt. Talvilaidunten ekonomien kantokyky on ilmeisesti ylitetty etelä- ja keskiosassa; syvä romahdus poromäärissä on todennäköistä, jos ruokinta lopetettaisiin. Pohjoisosassa voima-peräinen vasateurastus mahdollistaa tyydyttävän tuoton ilman ruokintaa. Pohjoisessa tuotto kasvoi pinta-alayksikköä kohden (poromäärät kasvoivat), etelässä kasvoi poroa kohti laskettu tuotto.

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Introduction

At the equilibrium of economic carrying capacity, the optimal animal density permits maximum production (Caughley, 1976). High animal densities and consequent range deterioration are commonly associated with intensive reindeer management, and may result in increased juvenile mortality and low carcass weights (Skogland, 1983; 1985). In the reindeer management area of Finland, biomass of the most preferred winter food, terricolous lichens (*Cladina* spp.), is far below the biomass that provides maximum production of lichen (Helle *et al.*, 1990). Reindeer can partly compensate for low biomass of terricolous lichens by using arboreal lichens or vascular plants (Laws, 1981; Leader-Williams, 1988), but shortages of lichens can increase likelihood of population crashes during severe winters. Occasional mass-deaths and consequent large-scale fluctuations in reindeer numbers were common in Finnish reindeer management during the 1960's and in the early 1970's. During 1974–1987, no substantial crash occurred, and the density of reindeer doubled without an increase in mortality or decrease in reproductive rate. Two plausible reasons exist for such a development (Helle & Säntti, 1982; Helle & Kojola, 1991). First, male-skewed calf harvest has reduced the number of calves and males, both of which are more susceptible than females to starvation in winter (Klein, 1968; Leader-Williams, 1980; Skogland, 1985). Second, supplemental food was provided in southern and central herds, where number of reindeer per range suitable for terricolous lichens was higher and biomass of lichens consequently lower than in northern herds (Helle *et al.*, 1990).

Maximum meat production is the main objective of Finnish reindeer management. Here we evaluate meat production per unit area and per reindeer at different levels of animal density, supplemental feeding, and variable calf harvesting.

Study area and methods

Study area.

There are 56 herding associations (herds) in the reindeer management area of Finland (Fig. 1). Areas of herding associations varied from 558 to 5580 km². Traditionally, reindeer in the northern part of the management area seek for food from below the snow during the whole winter, while in the south shift to arboreal lichens during the course of winter. We divided herds into 3 regional groups by the length of the time during which reindeer obtain their forage from beneath the snow (Fig. 1). In the northern region this period is 7 months, in the central region appr. 5 months and in the southern region ca. 3 months (Helle & Saastamoinen, 1979; Helle & Tarvainen, 1984). Densities of reindeer doubled during 1974–1987; the increase was most pronounced in northern herds (Helle & Kojola, 1991). The government of Finland sets the maximum number of reindeer for each herding association every 10 years; in northern and central herds numbers were commonly exceeded in the 1980's. The amount of hay provided per reindeer increased from north to south.

Study period.

Here we evaluated the period from 1960 to 1987. Calf harvesting began in some central herds in the mid 1960's. After a major population crash in 1973 calf harvesting was intensified also in the north (Fig. 2). Supplemental winter feeding also began after this crash. The amount of supplemental food provided per reindeer was greater during the 1980's than 1970's (Fig. 2; Helle & Saastamoinen, 1979; Nieminen & Autto, 1989). When comparing herd means, we divided our study period further:
(1) 1960–1966 (very few calves harvested, no supplemental winter feeding) (2) 1967–1973 (some male calves harvested, no supplemental feeding, decreasing populations), (3) 1974–1980 (some calf harvest and supplemental feeding, increasing populations) (4) 1981–1987 (increased calf harvest and supplemental feeding, increasing populations). We calculated intraherd regressions from 1960 to 1973 and from 1974 to 1987.

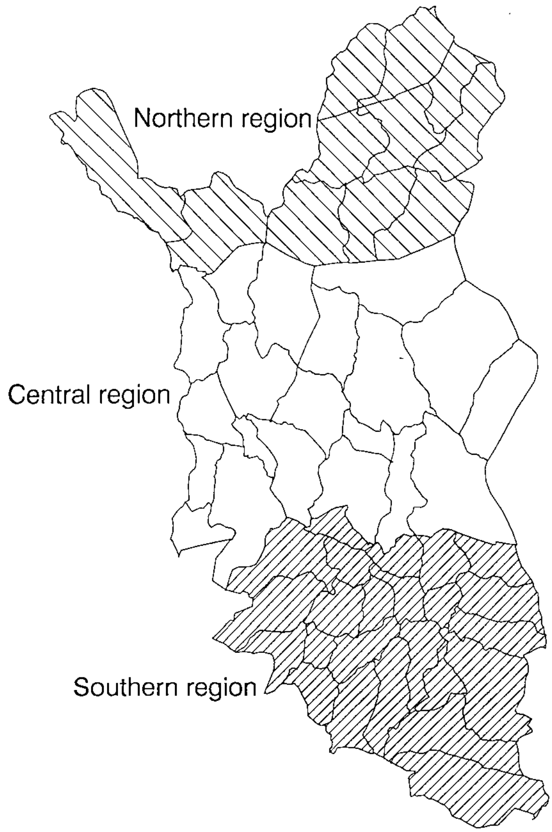

Fig. 1. Reindeer management area of Finland, divided into subareas used in this study. The period of digging for food from beneath the snow: northern herds 7 months, central herds 5 months, and southern herds 3 months.

Data collection.

We extracted numbers and harvest rates of reindeer from the archives kept by the Association of Reindeer Herders, and carcass weights of reindeer from the sales books maintained by meat buyers. Data com-

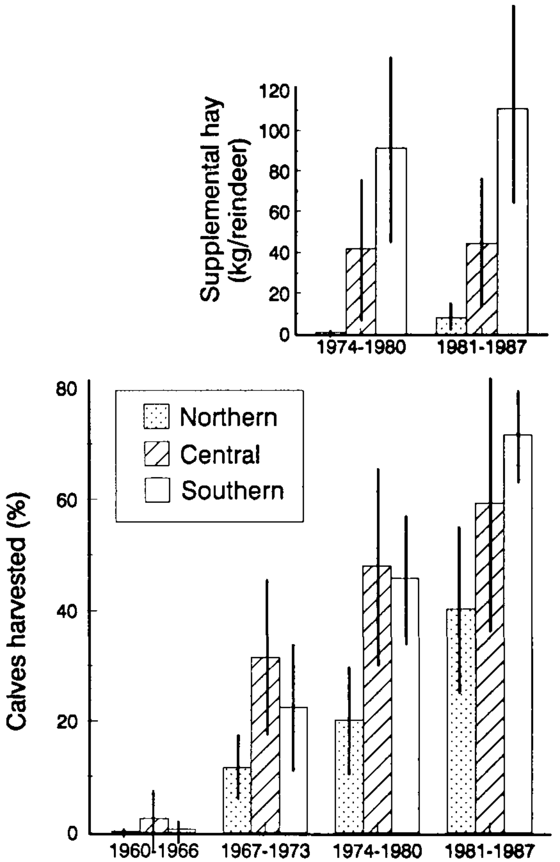

Fig. 2. The amount of supplemental hay provided per reindeer and the proportion of calves harvested (% of total number of calves) (means ± SD) in different parts of the reindeer management area of Finland. The amount of hay calculated from Helle & Saastamoinen (1979) and Nieminen & Autto (1989).

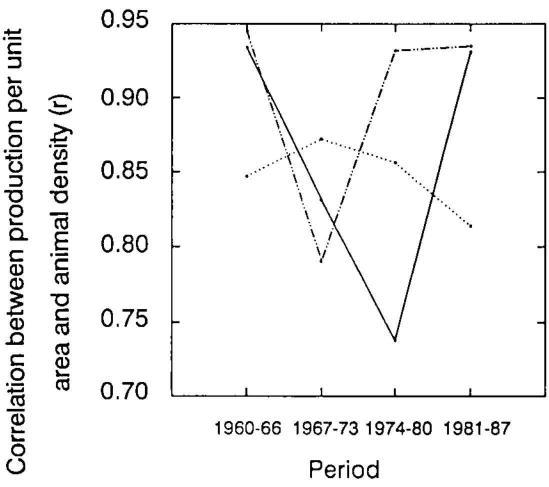

Fig. 3. Development of correlation between mean per unit area meat production and reindeer density within 3 subareas in Finland. Solid line indicates northern, dashed line central and plotted line southern herds.

prises of 1568 cases. The amounts of supplemental hay provided per reindeer were calculated from data published by Helle & Saastamoinen (1979) and Nieminen & Autto (1989). Round-ups and harvesting took place in early winter. Alaruikka (1964) estimated that in the early 1960's the proportion of uncounted reindeer was maximally 15% of all reindeer. During the late 1970's, the proportion of unmarked reindeer was 1–2% of all reindeer on the average (Autto, 1980; Niittyvuopio, 1981). We calculated per capita meat production by dividing the total meat production by the number of reindeer left after the round-up of the previous year. Round-ups and harvesting took place in early winter. When conducting analysis on the profitability of feeding, we used a producer price of 30 FIM kg^{-1} meat (the actual price in the mid 1980's) and 1 FIM kg^{-1} as a price of hay.

Statistical analysis.

Regional differences in meat production were tested by using oneway analysis of variance. The dependence of per capita and per unit area meat production on reindeer density, supplemental feeding and the rate of calf harvesting was tested by using simple and multiple regression analysis. To test whether

Table 1. Meat production per unit area in different parts of the reindeer management area of Finland. Regional differences were tested by oneway ANOVAs. Number of herds: southern 24, central 21 and northern region 11 herds.

Period	Meat production (kg/km^2) (mean, SD)			Regional Difference	
	Southern	Central	Northern	F	P
1960–1966	8.50 (3.84)	14.10 (5.72)	17.61 (7.35)	12.55	<0.001
1966–1973	9.26 (4.56)	11.59 (4.31)	18.27 (7.52)	11.54	<0.001
1974–1980	13.17 (5.16)	10.88 (4.21)	10.76 (5.98)	1.50	0.232
1981–1987	20.35 (8.49)	21.33 (7.51)	27.68 (12.96)	2.54	0.088

there existed regional differences in the frequency of positive correlations between density and production, we conducted Fisher's exact tests. The P values are from two-tailed tests. SYSTAT statistical software (Wilkinson 1988) was used for statistical procedures.

Results

Production per unit area

Inrease in meat production per unit area from the period 1974–1980 to 1981–1987 was most pronounced in northern herds, and reached a value higher than elsewhere (Table 1). Interherd correlation between production and reindeer density appeared to fluctuate less in southern than in central or northern herds (Fig. 3). In 1974–1980 calf harvesting influenced production per unit area only in the southern region, while in 1981–1987 production depended on calf harvesting both in the southern and northern region (Table 2). For the entire range, calf harvesting was influental during both of these periods (Table 2). Supplemental feeding did not affect significantly production in any multiple regression models fitting results for meat production per unit area (Table 2).

In 1960–1973, inter-year variation of meat production within herds was correlated positively ($P < 0.05$) with density in 34.5% of all herds ($n = 56$). In 1974–1987 this proportion was 73.2%. The change

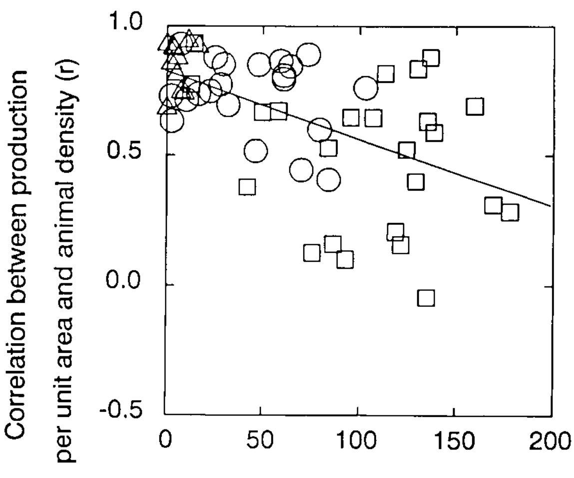

Fig. 4. Relationship between correlation of meat production per unit area with reindeer density and the intensity of supplementary feeding in 1974–1987 in Finland. Each point represents one herd. Triangles indicate northern, circles central and quadrats southern herds ($Y = 0.823 - 0.003 \times X$, $r = -0.570$, $n = 56$, $P < 0.001$).

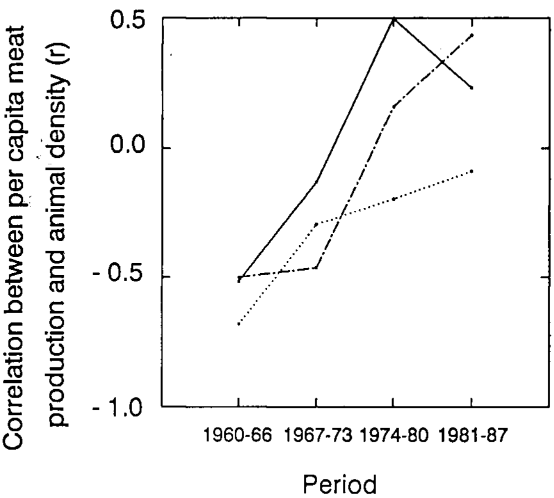

Fig. 5. Development of correlation between mean production per reindeer and animal density within 3 subareas in Finland. Solid line indicates northern, Dashed line central and plotted line southern herds.

was significant in northern ($P < 0.001$, $n = 11$) and central ($P < 0.002$, $n = 21$) herds but not in southern herds ($P = 0.386$, $n = 24$).

During 1974–1987, intraherd correlation between meat production and animal density was negatively correlated with the amount of hay given per reindeer during the winter (Fig. 4). This correlation also was correlated significantly with the mean rate of calf harvesting ($r = -0.386$, $n = 56$, $P < 0.001$).

Production per Reindeer

Meat production per reindeer increased clearly from 1974–1980 to 1981–1987. Per capita meat production was highest in the southern herds (Table 3). The correlation between per capita meat production and animal density changed from negative to positive from 1960–1966 to 1981–1987 (Fig. 5). In 1967–1973 mean production was independent of density and calf harvesting in northern and southern herds; in 1981–1987 density was positively correlated with per capita production in each region (Table 4). For the entire management area, calf harvesting in 1981–1987 (71.7%) explained more variation in productivity between herds than in 1974–1980 (26.2%, Fig. 6). Calf harvesting influenced productivity most clearly when more than 40% of calves were harvested (Fig. 6). Supplemental feeding explained 7.9% ($r = 0.282$, $P = 0.035$) of the interherd variation in productivity in 1974–1980. The corresponding figure was 23.7% in 1981–1987 ($r = 0.561$, $P = 0.001$). Feeding influenced productivity

Table 2. Multiple regression models fitting results for meat production per unit area (kg/km²) and the analysis of variance for the full regression. Density: Winter density (reindeer/km² land area); Calf harvesting: the proportion of calves harvested (% of total number of calves); Supplemental feeding: the amount of supplemental hay (kg/reindeer).

Period	Region	Independent variable	Coefficient	Standard error	Standard coefficient	T	P
1974–1980	Northern	Intercept	–0.774	3.244			
		Density	7.060	2.072	0.743	3.407	0.011
		Calf harvesting	0.115	0.126	0.185	0.915	0.391
		Supplemental feeding	–0.427	0.682	–0.129	–0.625	0.552
		R^2 = 0.665 F = 7.631, n = 11, P = 0.013					
	Central	Intercept	–1.245	2.278			
		Density	10.113	1.171	0.906	8.639	<0.001
		Calf harvesting	–0.007	0.041	–0.015	–0.160	0.875
		Supplemental feeding	–0.006	0.013	–0.051	–0.474	0.641
		R^2 = 0.848, F = 38.076, n = 21, P <0.001					
	Southern	Intercept	–5.893	2.290			
		Density	7.040	1.152	0.652	6.113	<0.001
		Calf harvesting	0.238	0.046	0.532	5.237	<0.001
		Supplemental feeding	–0.009	0.012	–0.076	–0.708	0.487
		R^2 = 0.780, F = 28.104, n = 24, P <0.001					
	Entire range	Intercept	–2.730	1.479			
		Density	8.246	0.812	0.768	10.159	<0.001
		Calf harvesting	0.093	0.029	0.274	3.209	0.002
		Supplemental feeding	0.002	0.009	0.021	0.248	0.805
		R^2 = 0.688, F = 41.445, n = 56, P <0.001					
1981–1987	Northern	Intercept	–27.117	4.320			
		Density	12.990	1.287	0.804	10.094	<0.001
		Calf harvesting	0.573	0.103	0.663	5.550	0.001
		Supplemental feeding	–0.304	0.227	–0.166	–1.343	0.221
		R^2 = 0.944, F = 57.261, n = 11, P <0.001					
	Central	Intercept	–15.334	6.330			
		Density	16.215	1.402	1.062	11.562	<0.001
		Calf harvesting	0.126	0.088	0.113	1.436	0.169
		Supplemental feeding	0.038	0.022	0.159	1.747	0.099
		R^2 = 0.891, F = 55.408, n = 21, P <0.001					
	Southern	Intercept	–22.754	3.404			
		Density	13.630	0.816	0.870	16.698	<0.001
		Calf harvesting	0.322	0.047	0.300	6.850	<0.001
		Supplemental feeding	0.011	0.009	0.060	1.139	0.268
		R^2 = 0.957, F = 171.500, n = 24, P <0.001					
	Entire range	Intercept	–23.841	2.456			
		Density	14.390	0.561	1.122	25.629	<0.001
		Caalf harvesting	0.343	0.034	0.537	10.104	<0.001
		Supplemental feeding	0.001	0.008	0.003	0.067	0.947
		R^2 = 0.923, F = 219.516, n = 56, P <0.001					

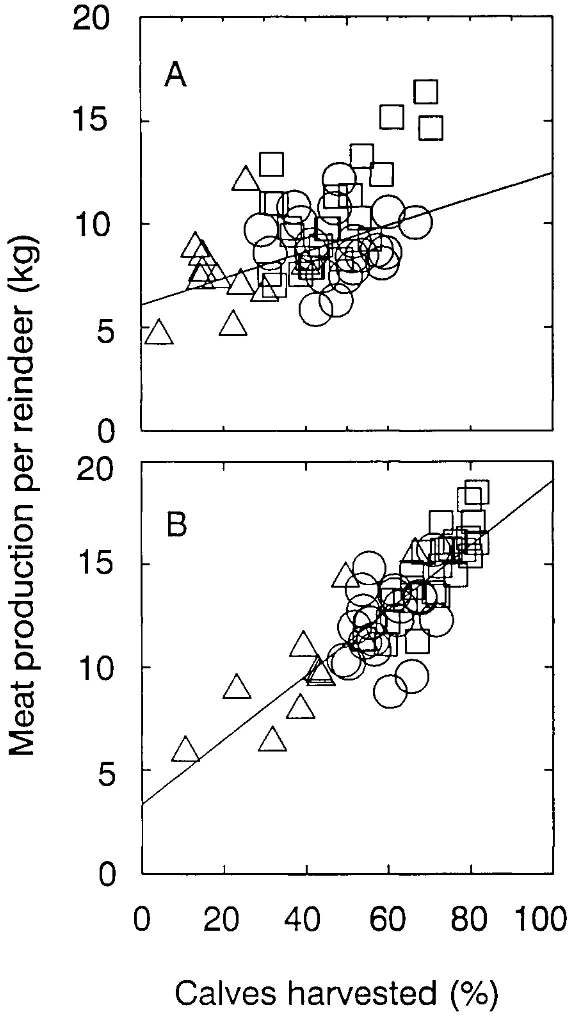

Fig. 6. Relationship between average of per capita meat production and the mean rate of calf harvesting in Finland. Each point represents one herd. Triangles indicate northern, circles central and quadrats southern herds. 1974-1980 (A): Y = 5.893 + 0.160xX, r = 0.512, n = 56, P < 0.001, 1981-1987 (B): Y = 3.171 + 0.082xX, r = 0.841, P < 0.001.

less than reindeer density or the rate of calf harvesting. Neither in regional multiple regression models nor in models for the entire management range meat production per reindeer depended significantly on the intensity of supplemental feeding (Table 4). When the cost of feeding was deducted from the income from reindeer meat, the residual income was not correlated with the amount of hay given each reindeer (1974–1980: r = –0.246, P = 0.068, 1981–1987: r = –0.121, P = 0.375).

Discussion

Productivity and range conditions

Data on production are available for comparison only from hunted populations of Norwegian wild mountain reideer (Gaare & Skogland, 1980; Skogland, 1986), which live mostly in open habitats and are of the same genetic origin as the wild ancestors of Finnish semi-domesticated reindeer (Siivonen, 1975; Nieminen & Helle, 1980). In wild reindeer, the maximum sustained yield of 14 kg meat km^{-2} is obtained at a population density of 1.75 reindeer km^{-2} (Skogland, 1986). These estimates suggest that without earlier over-grazing, the area associated with subtle lichen forage, comprises 12% of the total herd land area.

In southern and central herds in our study area, the proportion of area suitable for lichen was similar to that in Norway. In the 1960's and 1970's, before the initiation of intense supplemental feeding, meat production per unit area was substantially lower in the central and southern ranges than in Norway. Despite a lower animal density (Helle *et al.*, 1990), production exceeded the Norwegian level in the 1980's. In the north, where the Norwegian level was clearly exceeded during the 1980's, the winter range: total range ratio was considerably higher than that in Norway (Mattila, 1981).

Table 3. Meat production per reindeer in different parts of the reindeer management area of Finland. Regional differences were tested by oneway ANOVAs. Number of herds: southern 24, central 21 and northern region 11 herds.

Period	Meat production (kg/reindeer) (mean, SD)			Regional Difference	
	Southern	Central	Northern	F	P
1960–1966	10.64 (2.53)	11.37 (2.61)	10.47 (2.68)	0.62	0.622
1967–1973	8.95 (2.22)	9.42 (2.35)	14.11 (3.56)	16.49	<0.001
1974–1980	10.46 (2.57)	8.88 (1.52)	7.53 (1.98)	7.85	0.001
1981–1987	14.78 (2.05)	12.25 (1.71)	10.01 (15.50)	20.17	<0.001

Table 4. Multiple regression models fitting results for meat production per reindeer (kg) and the analysis of variance for the full regression. Density: Winter density (reindeer/km² land area); Calf harvesting: the proportion of calves harvested (% of total number of calves); Supplemental feeding: the amount of supplemental hay (kg/reindeer).

Period	Region	Independent variable	Coefficient	Standard error	Standard coefficient	T	P
1974–1980	Northern	Intercept	6.540	0.596			
		Density	−0.038	1.338	−0.012	−0.028	0.978
		Calf harvesting	−0.060	0.081	0.294	0.743	0.482
		Supplemental feeding	−0.209	0.440	−0.191	−0.474	0.650
		$R^2 = 0.000$ $F = 0.277$, $n = 11$, $P = 0.840$					
	Central	Intercept	6.449	1.981			
		Density	2.125	1.081	0.527	2.088	0.052
		Calf harvesting	−0.007	0.035	−0.043	−0.191	0.851
		Supplemental feeding	−0.002	0.012	−0.048	−0.185	0.856
		$R^2 = 0.209$, $F = 6.295$, $n = 21$, $P = 0.021$					
	Southern	Intercept	5.304	1.676			
		Density	−1.763	0.843	−0.327	−2.092	0.049
		Calf harvesting	−0.172	0.033	0.768	5.159	<0.001
		Supplemental feeding	−0.005	0.009	−0.090	−0.571	0.574
		$R^2 = 0.526$, $F = 9.512$, $n = 24$, $P < 0.001$					
	Entire range	Intercept	6.084	1.095			
		Density	−0.140	0.601	−0.028	−0.233	0.816
		Calf harvesting	0.078	0.021	0.489	3.626	0.001
		Supplemental feeding	0.003	0.006	0.055	0.410	0.684
		$R^2 = 0.223$, $F = 6.267$, $n = 56$, $P = 0.001$					
1981–1987	Northern	Intercept	−1.501	1.254			
		Density	1.738	0.373	0.471	4.652	0.002
		Calf harvesting	0.174	0.030	0.882	5.811	0.001
		Supplemental feeding	−0.009	0.066	−0.021	−0.132	0.899
		$R^2 = 0.910$, $F = 34.558$, $n = 21$, $P < 0.001$					
	Central	Intercept	1.437	3.812			
		Density	2.063	0.850	0.593	2.443	0.026
		Calf harvesting	0.107	0.053	0.420	2.025	0.059
		Supplemental feeding	0.021	0.013	0.397	1.653	0.117
		$R^2 = 0.237$, $F = 3.097$, $n = 11$, $P = 0.055$					
	Southern	Intercept	−0.259	2.128			
		Density	−0.942	0.510	−0.248	1.845	0.080
		Calf harvesting	0.219	0.029	0.841	7.434	<0.001
		Supplemental feeding	0.006	0.006	0.149	1.095	0.286
		$R^2 = 0.712$, $F = 19.998$, $n = 24$, $P < 0.001$					
	Entire range	Intercept	0.669	1.336			
		Density	0.812	0.305	1.214	2.659	0.010
		Caalf harvesting	0.175	0.018	0.929	9.502	<0.001
		Supplemental feeding	0.002	0.005	0.045	0.506	0.615
		$R^2 = 0.738$, $F = 52.732$, $n = 56$, $P < 0.001$					

In wildlife systems herbivore abundance is often controlled by the amount of high quality food in a critical season (Sinclair, 1975; Skogland, 1985). The basic difference between the Norwegian model and Finnish practice is the condition and role of lichen ranges. In Norway, a gross density of 1.75 reindeer km^{-2} allows maximum lichen production, providing reindeer with terricolous lichens to feed on the whole winter season. In southern and central herds in Finland, scarcity of terricolous lichens force reindeer to forage on arboreal lichens in mid and late winter. Lichen ranges were heavily overgrazed already in the beginning of this century (Anon., 1914). In northern herds overgrazing was reported in the 1950's and 1960's (Andreev, 1971). By the 1970's overgrazing in the north had reduced the biomass far below necessary for maximal rate lichen prodution (Helle *et al.*, 1990). Substitute foods for lichens in mountain areas consist mainly of sedges, grasses and dwarf-shrubs (Helle, 1984).

Negative correlations between density and per capita meat production within herds in the periods 1960–1966 and 1967–1973 were obvious indications of food limitation. Each herd experienced several crashes in the 1960's and 1970's (Helle & Kojola, 1991). The crash was followed by a period of increase in the herd size until the next crash. As a consequence, animal density peaked prior to a year of high mortality and low productivity. This may explain why meat production per unit area did not correlate with density in 1960–1973. A proximate reason for the crashes was adverse snow conditions (Helle & Säntti, 1982), but the ultimate reason was density-dependent food-limitation.

Positive correlation between per capita production and reindeer density in 1974–1980 and 1981–1987 was no doupt partly due to exceedings of the maximum permitted number of reindeer: when herd size outnumbered the legal limit, a higher proportion of reindeer was culled. In 1960–1966, when the relationship between per capita production and density were negative in each region, the size of the herds was usually below the number maximally permitted.

The improvement of the condition of lichen ranges by means of reducing reindeer density has not been considered as a realistic option in southern and central herds. An estimate of the biomass is 10 tons km^{-2} (Mattila, 1988), whilst in its most productive condition it would be 9o tons km^{-2} (Kärenlampi, 1973). With an annual growth rate of 11%, achieving maximum lichen production would take about 30 years. Without perfect exclusion of grazing, this process would be longer. The linear type functional response of reindeer to lichen supply (White & Trudell, 1980; Skogland, 1980) suggests that when lichen vegetation begins to recover due to lowered density, reindeer shift to forage increasingly on lichens and thereby slow the growth of the lichen. Terricolous lichens are of greatest importance in northern herds because arboreal lichens are absent there. Because of higher initial biomass, 25 tons km^{-2} (Mattila, 1981) in the north, recovery would be faster than in southern and central herds. The heavy population crash in 1973 evoked awareness about range conditions and some herding associations reduced the highest permitted number of reindeer for the 1980's. However, the permitted herd sizes were exceeded by the middle of the decade, and the excesses were greatest in the north.

Supplemental feeding and calf harvesting

Supplemental feeding and calf harvesting were a more or less conscious response to range deterioration. In southern and central herds this was accelerated by a reduction of the arboreal lichens as a result of large-scale logging of old forests (Helle & Saastamoinen, 1979). In contrast to economically managed herds of reindeer (see Gaare & Skogland, 1980; Skogland, 1986), the main objectives of the herder in traditional pastoralism are not maximal yield and income but rather a subsistence supply and a large herd (Noy-Meir, 1981). In reindeer management, a large herd provides its owner with power and influence within the herding association (Ingold, 1980). In the 1960's and 1970's, reindeer owners shifted from a largely subsistence based way of life to a monetary economy that stresses stable income (Pelto, 1973; Ingold, 1980). A predictable annual yield is required in modern reindeer husbandry but cannot be achieved without careful management when winter ranges are poor of most preferred forage. Although the supplementary feeding and changes in the structure of the winter herd were known, doubling of the number of reindeer and production of meat was unpredictable. Our results indicate that in southern herds increased production was more clearly related to increased yield per reindeer than in central and northern herds, where the increase was more clearly related to increased reindeer density.

Effects of supplemental feeding and calf harvesting were difficult to distinguish decisively from each other. They both were initiated in southern herds and then intensified and spread towards the north at the same rate. Results from the multiple regression analysis used to compare these effects indicate that calf harvesting has a greater influence than feeding on production. These results are not, however, very conclusive because our model did not take into account that without supplemental feeding animal density should be substantially lower in southern and central herds. Because supplemental feeding at the same time compensated for the loss of natural food resources, it is impossible to isolate its effects. In addition, it is fair to assume a dependence between these independent variables: supplemental feeding enables high calf/female ratio (Helle & Kojola, 1991), which in turn is necessary for extensive calf harvest. In the southern region most reindeer owners are farmers and therefore able to obtain high per capita production by supplemental feeding at reasonable costs. In north herds, some feeding is necessary when snow conditions are exceptionally difficult. As stated by Noy-Meir (1981), intensive supplemental feeding has also considerable ecological consequences: «Where supplementary feeding becomes economically feasible this may induce further increases in the herd and lead to maintenance of a highly overabundant herbivore population on a severely overgrazed range.»

Harvesting of male calves was introduced into Finland from Russian experimental herds, and its original objective was to make space for females in winter herd (Alaruikka, 1964). With regards meat production, the resultant sex ratio (commonly 1 male to 10 females) provides the most feasible option (Arobio *et al.,* 1980). Since the mid 1970's in the south and the 1980's in the north, harvesting of female calves became necessary. Otherwise the killing of females in their best reproductive age would be the only way to keep the number of reindeer within legal limits (Lenvik, 1989).

We suggest that intensified calf harvesting is the most important reason for the recent increase in production in northern herds. Calf harvesting is a tool enabling maximal production of meat from a herd of reindeer (Arobio *et al.,* 1980). This results from the rapid growth of calves and their susceptibility to starvation in winter (Skogland, 1985). In an earlier paper we put forward a hypothesis that there exists another mechanism by which calf harvesting increases productivity (Kojola & Helle, 1991a). This was based on the finding that calf harvesting had a distinct positive effect on the subsequent year's calf/female ratio in northern herds, where reindeer dig for food from beneath the snow the whole winter. Calves commonly share feeding craters with their mother and thus the food made available by the mother (Kojola, 1989). The nutritional status of breeding females is therefore likely to improve if their calves are killed before winter (Kojola & Helle, 1991a). This furthermore may bring about better survival of subsequent year's calf: close relationship between maternal condition and offspring survival is well documented in reindeer (Rognmo *et al.,* 1984; Lenvik 1989). Despite low energy content and poor digestibility of sedges, grasses and dwarf-shrubs, females may overwinter in satisfactory condition when most calves are killed before winter. In northern herds, calf harvesting frees reindeer from density-dependent mortality and recruitment rate (Kojola & Helle, 1991b; 1991c). Time trends in carcass weights indicate a slight decrease in northern herds (Helle *et al.,* 1991).

In conclusion, there was no evidence of exceeding of the economic carrying capacity in the northern region although animal density in some herds reached figures higher than so far reported for any continental population (Helle & Kojola, 1991). The concept of carrying capacity is based on the ratio between natality and mortality (Caughley, 1976). Like most vertebrates, the mortality rate of reindeer depends on age and sex (Klein, 1968; Leader-Williams, 1980; Skogland, 1980; Reimers, 1983). A lower initial mortality and higher reproductive rate is achieved, and consequently, higher carrying capacity of the range was created in the northern region, by means of altering sex and age ratios in the winter herd.

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