ARCTIC
VOL. 46, NO. 1 (MARCH 1993) P. 72-77

Reproduction and Mortality of Finnish Semi-Domesticated Reindeer in Relation to Density and Management Strategies

T. HELLE[1] and I. KOJOLA[2]

(Received 23 October 1990; accepted in revised form 30 April 1992)

ABSTRACT. We assessed the effects of management strategies during 1960-73 relative to strategies used during 1974-87 on the reproduction and mortality of 56 semi-domesticated herds of Finnish reindeer (*Rangifer tarandus tarandus*). During 1960-73, reindeer fed exclusively on natural forage growing on their range, and reindeer were harvested mostly as adults. These strategies were modified starting in 1974 to include supplemental feeding in the southern part of the Finnish reindeer range and calf harvesting throughout the range. We found significantly higher calf/female ratios, lower mortality, and less variation in both calf/female ratios and mortality during 1974-87 than during 1960-73. These changes occurred in spite of increased animal density. Coefficients of variation in calf/female ratio and mortality were negatively correlated with the prevalence of mature spruce forests, which are rich in arboreal lichens. Mean calf/female ratio and mortality rate depended on reindeer density only in the southern region during 1960-73. During 1974-87 these did not depend on density in any region. Within herds, calf/female ratio did not depend on density in most cases (98%), while in the later period the relationship between calf production and density was positive in some cases (25%). Mortality depended more often on density during the earlier (46% of herds) than the later (23% of herds) period. Calf harvesting influenced mortality more than supplemental feeding and virtually freed reindeer from density-dependent limitations. Supplemental feeding was used to compensate for deterioration of range resulting from overgrazing and logging of mature forests rich in arboreal lichens.

Key words: reproduction, mortality, density dependence, reindeer, *Rangifer tarandus*, management, Finland

RÉSUMÉ. On a évalué les retombées des stratégies d'aménagement utilisées entre 1960 et 1973 par rapport à celles utilisées de 1974 à 1987 sur la reproduction et la mortalité de 56 troupeaux semi-domestiques de rennes finlandais (*Rangifer tarandus tarandus*). Au cours de la période allant de 1960 à 1973, les rennes se nourrissaient uniquement de fourrage naturel provenant de leur territoire, et le prélèvement des rennes s'effectuait en majorité sur des animaux adultes. À partir de 1974, ces stratégies ont été modifiées pour inclure un supplément à l'alimentation du renne finlandais dans la partie sud de son territoire ainsi que le prélèvement de jeunes animaux sur la totalité du territoire. On a trouvé qu'au cours de la période allant de 1974 à 1987, le taux veaux/femelles était considérablement plus élevé, la mortalité était bien moindre et les fluctuations dans le taux veaux/femelles comme dans la mortalité étaient moindres qu'au cours de la période allant de 1960 à 1973. Ces changements se sont produits en dépit d'une augmentation de la densité des animaux. Les coefficients de variation dans le taux veaux/femelles et la mortalité avaient une corrélation négative avec la prédominance de forêts d'épinettes matures, où abondent les lichens corticicoles. La moyenne du taux veaux/femelles et du taux de mortalité ne dépendait de la densité du renne que dans la partie méridionale entre 1960 et 1973. Entre 1974 et 1987, ces paramètres n'étaient fonction de la densité dans aucune région. Au sein des troupeaux, le taux veaux/femelles n'était pas fonction de la densité dans la plupart des cas (98 p. cent), alors que dans la deuxième période de l'étude, le rapport entre la production de veaux et la densité était positif dans quelques cas (25 p. cent). La mortalité dépendait plus souvent de la densité au cours de la première période de l'étude (45 p. cent) qu'au cours de la seconde (23 p. cent). Le prélèvement des veaux avait une influence sur la mortalité plus que ne l'avait le supplément à l'alimentation et libérait pratiquement le renne des restrictions dues à la dépendance de la densité. Le supplément à l'alimentation était utilisé comme compensation à la détérioration du territoire due au surpâturage et à l'exploitation forestière de forêts matures riches en lichens corticicoles.

Mots clés: reproduction, mortalité, fonction de la densité, renne, *Rangifer tarandus*, aménagement, Finlande

Traduit pour le journal par Nésida Loyer.

INTRODUCTION

The last three decades in the management of semi-domesticated reindeer in Finland can be divided roughly into two periods. Until the early 1970s, the early and mid-winter diet of reindeer in woodlands consisted mostly of terricolous lichens (*Cladina* sp.) and the late winter diet mostly of arboreal lichens (*Alectoria* and *Bryoria* sp.); on northern fell ranges alternative foods to overutilized lichens were dwarf shrubs, grasses and sedges (Alaruikka, 1964; R. Helle, 1966; T. Helle, 1984). Wide annual fluctuations in reindeer numbers occurred during the 1960s and early 1970s as a result of suggested density-dependent food limitation, which is commonly associated with intense reindeer management (Kärenlampi, 1973; Skogland, 1986).

In the mid-1970s the use of dried hay as supplemental food spread rapidly throughout the reindeer management range of Finland, except in northernmost herds located north of the timber line (Helle and Saastamoinen, 1979). At the same time, calf harvest replaced the harvest of yearling and adult males. The original purpose of calf harvest was to optimize herd structure for meat production (Arobio *et al.*, 1980; Lenvik, 1989). Because calves are more susceptible than adults to winter mortality from starvation (Leader-Williams, 1980), calf harvesting may reduce winter mortality.

This study deals with reproduction and natural mortality of semi-domesticated reindeer in Finland. We compare two periods and evaluate how density, supplemental feeding and calf harvest have influenced reproductive and mortality rates under different range conditions.

STUDY AREA AND METHODS

The reindeer range in Finland is divided into 56 management areas, varying from 558 to 5580 km^2. Each management area is occupied by a discrete herd of reindeer that is managed by a herding association.

Range data were obtained from a survey carried out as a part of the Finnish National Forest Inventory in 1976-78 and 1982-84 (Mattila, 1981, 1988). Biomass (terricolous lichens) or relative abundance (arboreal lichens) were estimated from a field sample consisting of 32 820 quadrats from 3282 randomly selected sites. Additionally, these range data provided quite reliable estimates of the area of most common types of winter ranges. In the late 1970s terricolous lichen biomasses in dry sites in southern,

[1]The Finnish Forest Research Institute, Eteläranta 55, SF-96300 Rovaniemi, Finland
[2]Finnish Game and Fisheries Research Institute, Game Division, Meltaus Game Research Station, SF-97340 Meltaus, Finland

central and northern regions were on average 70, 150 and 300 kg dry weight per ha respectively (Mattila, 1981); the biomass at which lichens are maximally productive is about 1000 kg per ha (Kärenlampi, 1973). In the southern region ranges most suitable for terricolous lichens were heavily overgrazed by the beginning of this century (Anon., 1914). In woodland ranges reindeer switch to arboreal lichens over the course of winter (Helle and Saastamoinen, 1979). We divided the herds into three regional groups by the length of the period when reindeer obtain forage from beneath the snow (Fig. 1). For the northern region (n = 11 herds) this period is *ca.* 7 months, the central region (n = 21 herds) *ca.* 5 months and the southern region (n = 24 herds) *ca.* 3 months (Helle and Saastamoinen, 1979; Helle and Tarvainen, 1984).

After a population crash in 1973 (Fig. 2), supplemental feeding became prevalent in central and southern regions. Therefore, we divided the study period into two periods: 1960-73 and 1974-87. Exact data on supplemental feeding were available for five years: 1975, 1977, 1985, 1986 and 1987. The mean amount of hay fed per animal during winter was 5.7 kg (0-16.4 kg) in northern herds, 43.9 kg (2.2-103.1 kg) in the central part and 104.5 kg (12.7-177.6 kg) in southern herds (calculated from Helle and Saastamoinen, 1979, and from Nieminen and Autto, 1989).

The number and harvest rates of reindeer were extracted from the archives kept by the Association of Reindeer Herders. Calves were counted and ear-marked in midsummer, and harvesting took place in early winter. We calculated the annual mortality rate by calculating the change from the post-harvest number of reindeer to the pre-harvest count of the subsequent year (calves born between counts were excluded). The accuracy of counts might vary somewhat between years, but large uncounted herds have not existed (Alaruikka, 1964). In 1979, 1980 and 1981, for example, the proportion of unmarked animals (mainly yearlings) was 1.3, 1.2 and 1.0% respectively, and this proportion did not show a regional pattern (Autto, 1980; Niittyvuopio, 1981). The effect of great predators, such as wolves (*Canis lupus*), wolverines (*Gulo gulo*) and brown bears (*Ursus arctos*), was so marginal (according to the official statistics they killed maximally 2% of reindeer annually) that it was not considered in this study. If not otherwise specified, the density of reindeer is the number of animals per km² land area. To evaluate the availability of arboreal lichens, we calculated the proportion of old spruce forest (most abundant source of arboreal lichens) of the total area of range.

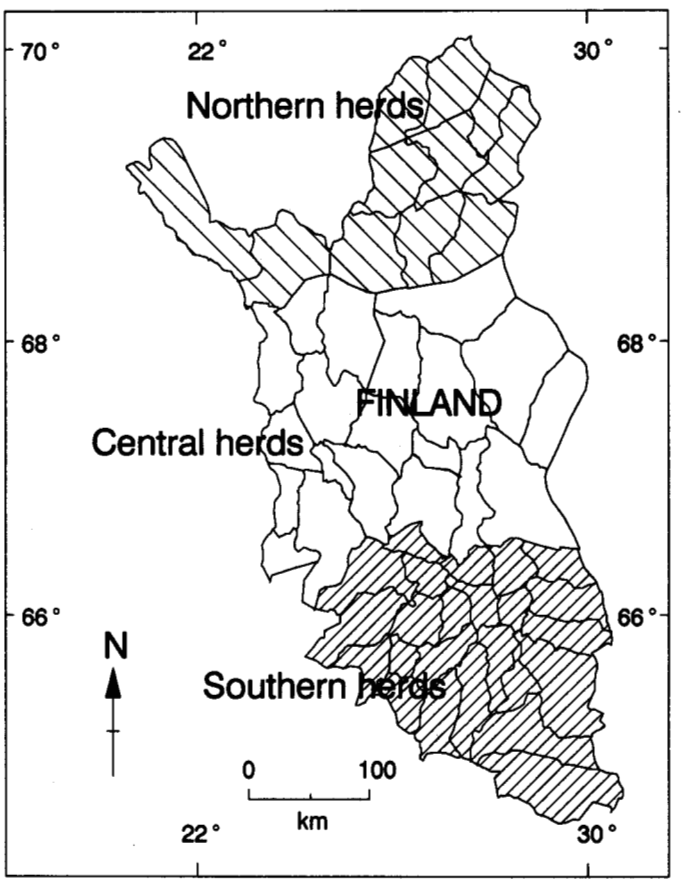

FIG. 1. Subdivision of reindeer management range of Finland into different regions.

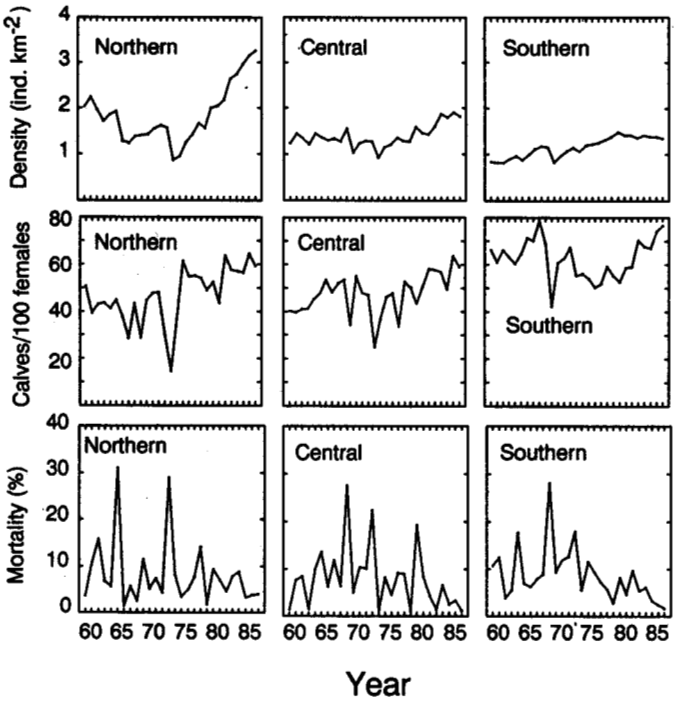

FIG. 2. Gross density, calf/female ratio and mortality in semi-domesticated reindeer in Finland.

We studied density dependence of calf/female ratio and mortality separately for each herd. Herd means of calf/female ratio, mortality and reindeer density from 1960-73 and 1974-87 were used when studying density dependence within different regions and within the total range. We assessed density dependence by using simple regression models. The influence of supplemental feeding, calf harvesting and the prevalence of mature spruce-dominated woodland on calf/female ratio and mortality, as well as their variability, was calculated by using simple and multiple regression. The adjusted R-square, sample size and probability are reported for each model. The relationship between the amount of hay per reindeer and reindeer density per winter range was evaluated by using a Pearson correlation analysis. Regional differences were tested by use of one-way analysis of variance and period difference with a paired t-test. Coefficients of variation (CV) were compared by use of Kruskal-Wallis one-way tests and Wilcoxon matched pairs tests. All the P values presented are from two-tailed tests.

RESULTS

Reproduction

During 1960-73, calf/female ratios were highest in the southern region and lowest in the northern region (Table 1). During 1974-87 these ratios were lowest in the central region (Table 1).

TABLE 1. Changes in the mean calf/female ratio and natural mortality of semi-domesticated reindeer from 1960-73 to 1974-87 in Finland[1]

Calves/100 females	1960-73		1974-87		Period difference		
Region	Mean	SD	Mean	SD	t	df	P
Northern	37.6	8.1	54.7	7.4	7.41	11	<0.001
Central	45.1	10.5	50.4	2.6	2.15	21	0.044
Southern	48.7	6.0	60.9	4.4	8.95	24	<0.001
Regional difference			F = 6.66 df = 1,54 P < 0.001		F = 29.34 df = 1,54 P < 0.001		

Natural mortality (%)	1960-73		1974-87		Period difference		
Region	Mean	SD	Mean	SD	t	df	P
Northern	11.0	3.7	6.0	3.2	2.26	11	0.047
Central	9.8	3.9	5.2	1.7	3.11	21	0.006
Southern	11.0	3.7	5.6	2.9	9.28	24	<0.001
Regional difference			F = 0.67 df = 1,54 P = 0.515		F = 2.93 df = 1,54 P = 0.272		

[1]Differences between periods were tested by use of paired t-tests, and differences between regions by use of one-way ANOVA from herd means.

Within herds, the annual calf/female ratio depended on density (probability from linear regression <0.05) in one case in the earlier period, while in the other herds (n = 55) it was density independent. In 1974-87 calf/female ratios were positively correlated with density in 25% of the herds; in other herds calf/female ratios were not correlated with density.

Mean calf/female ratios (%) for the period 1960-73 did not, however, depend significantly on the proportion of mature spruce forests with high arboreal lichen biomass ($y = 59.20 - 0.165X$, adjusted $R^2 = 0.035$, $n = 56$, $P = 0.166$). Mean calf/female ratios during 1960-73 depended on mean density in the southern region, but were density independent in other regions (north: $y = 30.56 + 4.29X$, $R^2 = 0.037$, $n = 11$, $P = 0.269$; central: $y = 44.09 + 0.80X$, $R^2 = 0.000$, $n = 21$, $P = 0.874$; south: $y = 53.39 - 4.86X$, $R^2 = 0.140$, $n = 24$, $P = 0.040$). During 1974-87 this ratio was density independent in each region (north: $y = 45.74 + 4.47X$, $R^2 = 0.086$, $n=11$, $P = 0.197$; central: $y = 47.70 + 1.82X$, $R^2 = 0.029$, $n = 21$, $P = 0.222$; south: $y = 63.89 - 2.28X$, $R^2 = 0.026$, $P = 0.217$).

Natural Mortality

Mortality rates were significantly lower in the later than in the earlier period (Table 1). Within-herd mortality depended on reindeer density (probability from linear regression model <0.05) in 45% of herds during 1960-73 and in 23% of herds (n = 56) during 1974-87. Mortality did not vary significantly by region (Table 1). Mean mortality rate (%) during 1960-73 depended on density only in the southern region (north: $15.80 - 2.94X$, $R^2 = 0.228$, $n = 11$, $P = 0.078$; central: $y = 7.09 + 2.07X$, $R^2 = 0.015$, $n = 21$, $P = 0.269$; south: $y = 7.25 + 3.91X$, $R^2 = 0.263$, $n = 24$, $P = 0.006$), and during 1974-87 mortality rate did not depend on density in any region (north: $y = 4.47 + 0.76X$, $R^2 = 0.000$, $n = 11$, $P = 0.629$; central: $y = 4.14 + 0.73X$, $R^2 = 0.000$, $n = 21$, $P = 0.462$; south: $y = 5.45 + 0.09X$, $R^2 = 0.000$, $n = 24$, $P = 0.944$).

Variability of Reproduction and Mortality

The coefficient of variation (CV) within herds was greater in the earlier than in the later period in the northern and central regions (Table 2). Differences among regions were significant but less pronounced in the later period (Table 2). In the earlier period, CVs of calf/female ratios were negatively related to the proportion of mature spruce forests ($y = 0.164 - 0.201X$, $R^2 = 0.119$, $n = 56$, $P = 0.005$). In the later period no significant dependence was found ($y = 0.226 - 0.088X$, $R^2 = 0.003$, $n = 56$, $P = 0.316$). The CVs of mortality differed significantly among regions and were highest in the northern region during both periods (Table 2). In the earlier period the CVs of mortality were negatively related to the proportion of mature spruce-dominated woodland ($y = 0.963 - 1.473X$, $R^2 = 0.200$, $n = 56$, $P < 0.001$). In the later period CVs were dependent on both the proportional area of such woodland ($y = 0.650 - 0.728X$, $R^2 = 0.149$, $n = 56$, $P = 0.002$) and the amount of hay fed per reindeer ($y = 0.600 - 0.002X$, $R^2 = 0.163$, $P = 0.001$).

TABLE 2. Coefficients of variation for calf/female ratio and natural mortality of semi-domesticated reindeer during 1960-73 and 1974-87 in Finland[1]

CV of calf/female ratio	1960-73		1974-87		Period difference		
Region	Mean	SD	Mean	SD	z	n	P
Northern	0.34	0.08	0.22	0.08	2.93	11	0.003
Central	0.34	0.10	0.23	0.04	3.58	21	<0.001
Southern	0.20	0.07	0.18	0.06	1.23	24	0.219
Regional difference			H = 24.43 P < 0.001		H = 5.91 P = 0.034		

CV of mortality	1960-73		1974-87		Period difference		
Region	Mean	SD	Mean	SD	z	n	P
Northern	0.93	0.37	0.57	0.17	2.85	11	0.004
Central	0.77	0.26	0.64	0.10	2.14	21	0.033
Southern	0.45	0.19	0.35	0.13	1.87	24	0.059
Regional difference			H = 22.73 P < 0.001		H = 30.18 P < 0.001		

[1]Differences between periods were tested by use of Wilcoxon matched pairs tests and differences between regions by use of Kruskal-Wallis tests from herd means.

Effects of Supplemental Feeding and Calf Harvesting

The amount of hay was negatively correlated with mean biomass of terricolous lichens ($r = -0.570$, $n = 56$, $p < 0.001$) and positively correlated with the number of reindeer per km² lichen range ($r = 0.576$, $n = 56$, $p < 0.001$).

Multiple regression analysis of the effects of density and supplemental feeding on mean calf/female ratios indicated that feeding influenced the calf/female ratio only in data pooled over the entire range (Table 3).

In a multiple regression model with density, supplemental feeding and the rate of calf harvest as independent variables, calf harvest influenced mean rate of mortality in the northern and southern region and in data pooled over the entire range, while supplemental feeding did not influence mortality in any region (Table 4). Mean rate of mortality depended on mean rate of calf harvest during 1974-87 but not during 1960-73, when substantially lower proportions of calves were harvested (Fig. 3). The influence of calf harvesting was greatest when more than 40% of calves were harvested (Fig. 3). The decrease in the mean mortality rate from 1960-73 to 1974-87 was related negatively to the mean increase in the rate of calf harvesting (Fig. 4).

DISCUSSION

Density Dependence

Density-dependent effects on reproductive rate and mortality in wild reindeer herds are well documented. Skogland (1985, 1989, 1990) found that neither fecundity nor adult survival were affected by density-dependent winter food limitation, but increasing density caused declines in survival of neonates and juveniles. Our index for reproductive rate (calf/female ratio in mid-summer) combined both birth rate per female and early survival of calves, and we were not able to specify mortality rates separately for juveniles and adults. Therefore, our results are not fully comparable to those obtained for wild reindeer.

Low neonatal survival was frequent during the 1960s and the early 1970s throughout the entire reindeer management range in Finland (Haukioja and Salovaara, 1978; Helle and Säntti, 1982). Winter mortality of juveniles and adults was high during this period during winters with difficult snow conditions (Helle and Säntti, 1982). Calf/female ratios were about 30% lower than in herds without density-dependent food limitation (Bergerud, 1980; Skogland, 1985).

Despite these signs of winter food limitation, reproduction or mortality rates appeared to be density dependent only in the southern region during the earlier period. However, the alternative explanation that the reproductive and mortality rates depended almost exclusively on density-independent climatic factors is not evident. Hard or deep snow might be a proximate cause for poor food availability, but the ultimate cause was low lichen biomass as a result of prolonged overutilization.

TABLE 3. Multiple regression models fitting results for mean calf/female ratio (%) in semi-domesticated reindeer in Finland during 1974-87 and the analysis of variance for the full regression[1]

Region	Intercept	Independent variable	Coefficient	Standard error	t	p
Northern	40.974	Density	5.609	3.489	1.607	0.147
		Supplemental hay	0.436	0.489	0.893	0.393
			$R^2 = 0.065$, F = 1.346, n = 11, P = 0.313			
Central	45.079	Density	2.915	1.867	1.561	0.136
		Supplemental hay	0.023	0.025	0.927	0.336
			$R^2 = 0.022$, F = 1.221, n = 21, P = 0.318			
Southern	65.143	Density	−0.727	2.101	0.346	0.733
		Supplemental hay	−0.032	0.024	1.339	0.192
			$R^2 = 0.061$, F = 1.747, n = 24, P = 0.199			
Entire range	52.582	Density	1.045	0.150	2.500	0.013
		Supplemental hay	0.067	0.016	4.282	<0.001
			$R^2 = 0.078$, F = 3.331, n = 56, P = 0.043			

[1]Sample sizes are the number of herds. Density as reindeer · km^{-2}, supplemental hay as kg·$reindeer^{-1}$.

TABLE 4. Multiple regression models fitting results for mean rate of natural mortality rate of semi-domesticated reindeer in Finland during 1974-87 and the analysis of variance for the full regression[1]

Region	Intercept	Independent variable	Coefficient	Standard error	T	P
Northern	9.933	Density	1.398	1.372	1.019	0.342
		Supplemental hay	0.173	0.229	0.753	0.476
		Calf harvesting	−0.255	0.102	2.509	0.040
			$R^2 = 0.316$, F = 2.543, n = 11, P = 0.140			
Central	8.009	Density	0.007	1.289	0.005	0.996
		Supplemental hay	−0.011	0.018	0.609	0.551
		Calf harvesting	−0.042	0.064	−0.657	0.520
			$R^2 = 0.000$, F = 0.557, n = 21, P = 0.651			
Southern	22.872	Density	1.055	0.780	1.354	0.191
		Supplemental hay	0.001	0.009	0.143	0.887
		Calf harvesting	−0.305	0.040	7.584	<0.001
			$R^2 = 0.708$, F = 19.560, n = 24, P <0.001			
Entire range	10.997	Density	−0.194	0.588	0.330	0.743
		Supplemental hay	0.015	0.008	1.971	0.054
		Calf harvesting	−0.116	0.029	3.948	<0.001
			$R^2 = 0.201$, F = 5.618, n = 56, P <0.001			

[1]Sample sizes are the number of herds. Density as reindeer · km^{-2}, supplemental hay as kg·$reindeer^{-1}$, calf harvesting as the proportion of calves harvested.

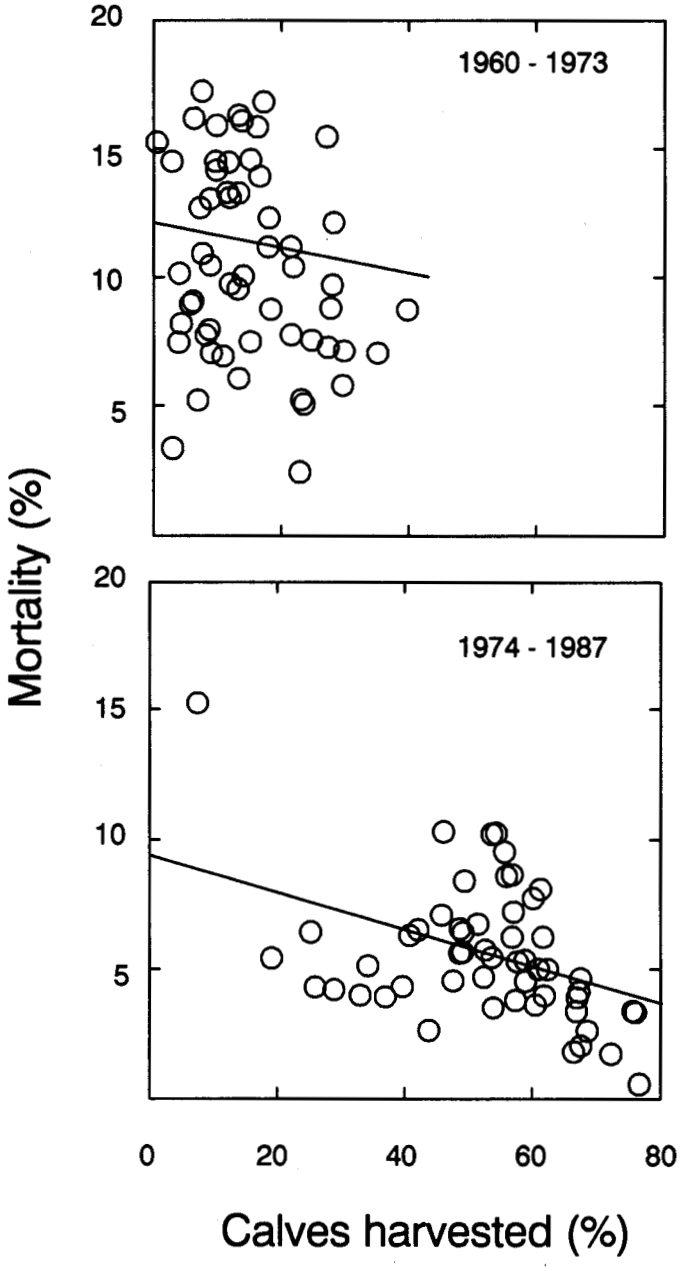

FIG. 3. Relationship between the mean rates of calf harvesting and natural mortality of semi-domesticated reindeer in Finland (1960-73: $y = 12.141 - 0.105X$, $R^2 = 0.062$, $n = 56$, $P = 0.066$; 1974-87: $y = 9.663 - 0.077X$, $R^2 = 0.179$, $n = 56$, $P = 0.001$).

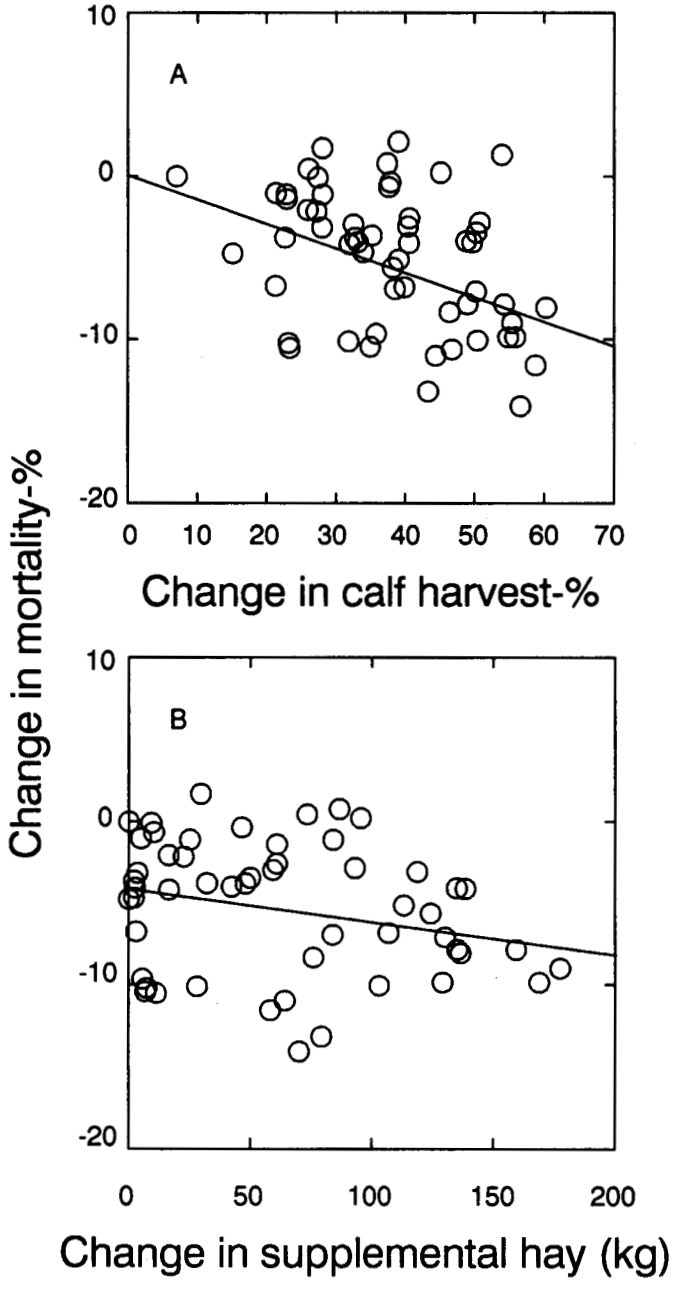

FIG. 4. Relationship between change in the harvest rate of calves and the mortality rate in Finnish reindeer (change from 1960-73 to 1974-87, $y = 0.419 - 0.144$, $R^2 = 0.161$, $n = 56$, $P = 0.001$).

Analysis of density dependencies is the first task for reasonable management of wild ungulate populations (Caughley, 1976). Models based on density dependence have been used successfully in the management of wild reindeer populations (Gaare and Skogland, 1980; Skogland, 1986). Our study showed that the usefulness of such an analysis for semi-domesticated reindeer is limited. This is due to the fact that the detection of density dependencies provides that variation in available food resources is wide enough to produce differences in reproduction and mortality. Reindeer ranges in northern Finland lack such variation because of intense grazing for several hundred years. The area of lichen range per reindeer varies, but scarcity of lichens has been compensated for in woodland regions by alternative food resources (Helle and Saastamoinen, 1979; Mattila, 1981). The question of density dependence is closely related to the way in which herd sizes were manipulated. The highest permitted number of reindeer for each herd was set every tenth year by the government of Finland. Those numbers were largely based on proposals made by the herding association in question and based on the condition and behaviour of animals. Repeated attempts by reindeer to emigrate from their own management range as well as population crashes in winter were interpreted as an indication of overloading of the ranges, which was taken into account when making decisions that consider herd size (Autto, 1980; Helle, 1981; Niittyvuopio, 1981). The experience of reindeer owners is consistent with Skogland (1985), who showed that emigration in wild reindeer is density dependent.

Within herds, density-dependent mortality was common in 1960-73. In many herds the density was maximum just before the common population crash in 1973. Some data suggested that lichen biomasses began decreasing due to overgrazing from the late 1950s onwards (Helle, 1980). Another explanation also exists. In older times, occasional mass deaths were a normal phenomenon; they were triggered by exceptionally difficult snow conditions. After a crash the herders began to increase the number of animals, and that continued to the next crash. That produces a pattern seemingly similar to density dependence.

The Effects of Calf Harvesting and Supplemental Feeding

The concept of carrying capacity is based on the ratio between natality and mortality in a herbivore population (Caughley, 1976). Our results indicate that calf harvest decreases winter mortality of reindeer, thereby increasing the carrying capacity of the range. Calf harvest may also improve the reproductive rate, because calves are likely to entail significant energetic costs for females during winter (Kojola and Helle, 1993). Our results indicate that calf harvest influenced mortality more than supplemental feeding. Supplemental feeding primarily compensates for overutilization of winter range and large-scale logging of mature spruce forests rich in arboreal lichens (Kautto *et al.*, 1986; Mattila, 1988). Intensive supplemental feeding has a positive effect on the body weight of reindeer (Helle *et al.*, unpubl.), but it did not decisively affect herd reproduction and mortality. The compensatory nature of supplemental feeding is evidenced by a close inverse relationship between the amount of hay provided per reindeer and density of reindeer on suitable lichen range, as well as lichen biomass (Helle *et al.*, 1990; Kojola *et al.*, unpubl.).

Management practices evaluated in this study are in use to a lesser extent in Sweden and Norway (Skjenneberg, 1989). Calf harvest, and possibly supplemental feeding, enable populations to increase without density-dependent effects, challenging conventional range studies based solely on range-reindeer interactions. The present trends increase meat production but lead to overutilization of natural ranges, as has been found in livestock raising (Noy-Meir, 1981).

ACKNOWLEDGEMENTS

We thank Thomas Hanley, Terje Skogland and three anonymous reviewers for valuable comments on the manuscript.

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