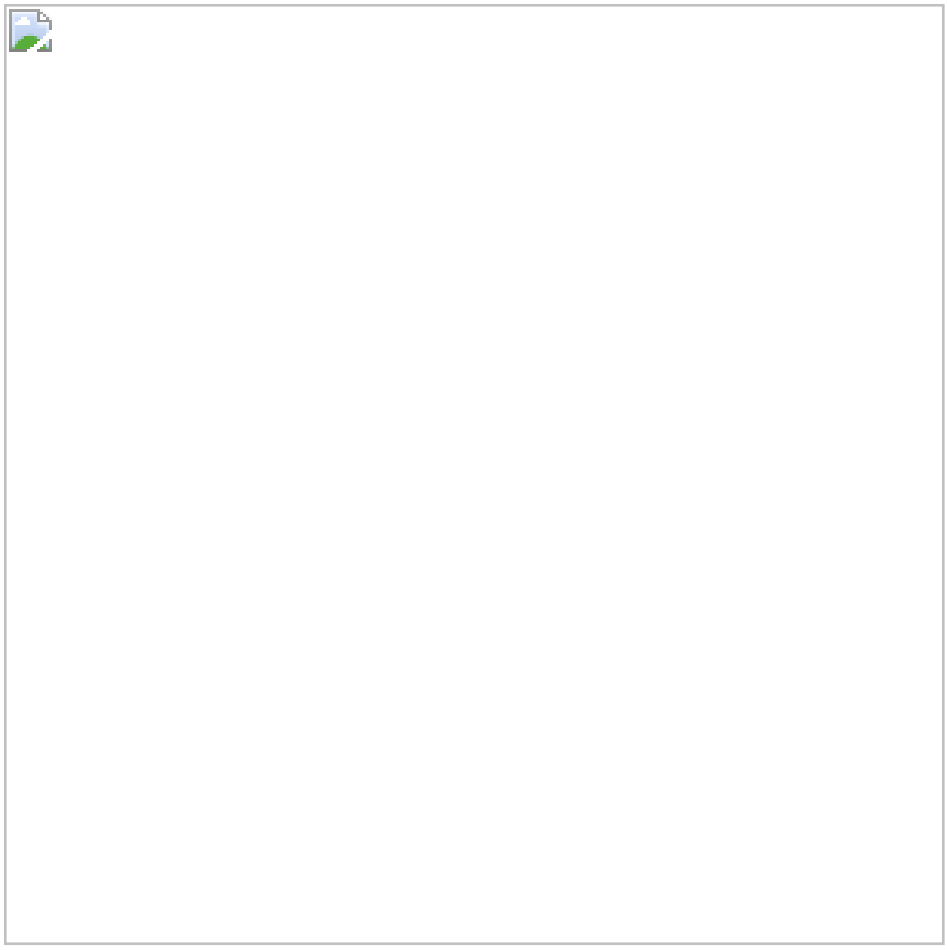

Effects of lichen biomass on winter diet, body mass and reproduction of semi-domesticated reindeer Rangifer t. tarandus in Finland

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Effects of lichen biomass on winter diet, body mass and reproduction of semi-domesticated reindeer *Rangifer t. tarandus* in Finland

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Winter food supply very likely influences the life history of reindeer *Rangifer t. tarandus*. We therefore examined how lichen biomass affects winter diet composition, body mass and reproduction in 14 herds of semi-domesticated reindeer in northern Finland. Diet composition was assessed microhistologically on faeces collected from the actual winter feeding sites of reindeer. When lichen was scarce at these sites reindeer included vascular plants and mosses in their diet. Calf dressed weight depended on both ground lichen biomass and the intensity of supplemental feeding, doe dressed weight depended on lichen biomass alone. One explanation for this difference between calves and does is the connection between food supply and calf mortality: low lichen biomass may promote newborn mortality, which, in turn, frees breeding females from investing further in current reproductive investment. Relative offspring weight (calf/female weight ratio) depended on both lichen biomass and supplemental feeding. Low lichen availability appeared to enhance the impact of density-independent factors on reproduction, because the annual variation in reproductive rate increased with decreasing lichen biomass.

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Intensive long-term utilisation by grazers often causes a decline in the biomass of the most preferred plant species until equilibrium is established (Helle & Aspi 1983, Bergström & Danell 1987, Vinton & Harnett 1992). Grazers may then begin to feed on lower-ranking foods, which may impair growth and lower gross recruitment rates (Skogland 1983, 1985, Fowler 1987). Reindeer *Rangifer t. tarandus* prefer lichens as their winter food (Bergerud 1972, Gaare & Skogland 1975, Helle 1981). Lichens are certainly not necessary for reindeer (Thomas & Edmonds 1983, Leader-Williams 1988), but both rumen analyses and food selection experiments indicate a profound preference for lichens to other food items (Skogland 1984a, Danell et al. 1994). Studies of wild herds indicate that overgrazing of ground lichens should increase the proportions of vascular plants and mosses in the diet (Klein 1968, Skogland 1984a, Klein 1990).

Lichens are poor in proteins and most macrominerals, but rich in soluble carbohydrates, which are an important source of maintenance energy in winter (Garmo 1986, Klein 1990). The high palatability of lichens is also associated with their high digestibility due to low cellulose and lignin contents (Garmo 1986, Danell et al. 1994). Use of lichens is energetically cheaper than use of vascular plants, because proteins increase water intake and thus thermal energy costs (Soppela et al. 1992). Where predators are controlled and seasonal migrations of reindeer restricted by natural or man-made barriers, ground lichens may be overgrazed (Klein 1968, Gaare & Skogland 1980, Helle et al. 1990). In some regions of northern Fin-

land, the lichen biomass in habitats suitable for lichen growth is very low owing to the high stocking rate by reindeer (Helle et al. 1990). In this paper we consider winter diet and evaluate some life history consequences of lichen availability to semi-domesticated reindeer in northernmost Finland. Evident consequences of low lichen supply are impaired growth and reproductive rates and increased impact of density independent factors (Skogland 1983, 1985).

Material and methods

Study areas

Data were collected on 14 free-ranging semi-domesticated reindeer herds in northernmost Finland. The predominant winter habitat in the four northernmost herds was treeless alpine heath; in the other herds it was mature Scots pine *Pinus sylvestris* forest (Fig. 1).

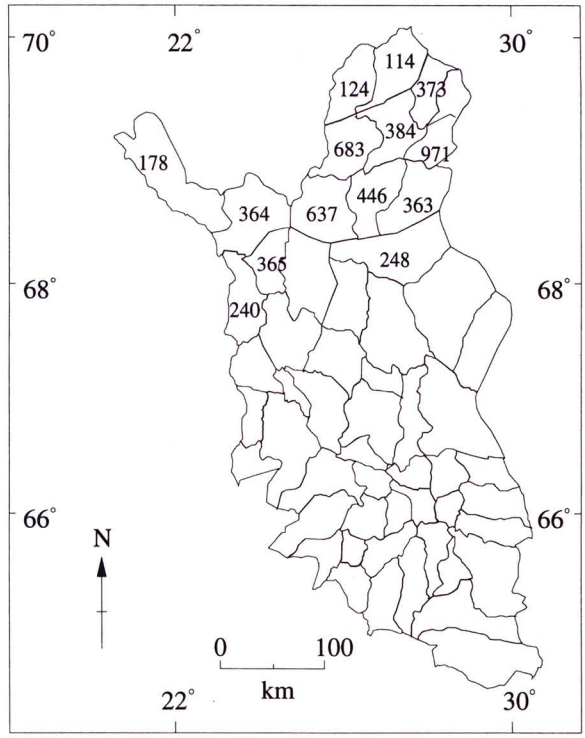

Figure 1. Mean ground lichen biomasses of *Cladonia* + *Sterocaulon* (kg DM/ha) in the 14 study herds at winter feeding sites of reindeer.

Variables

Diet composition

Diet composition was available for 13 herds. Diet was determined microhistologically at AAFAB, Composition Analysis Laboratory, Colorado, from 599 faecal pellet groups collected at 174 actual feeding sites in winter 1990-1991. Faecal data collection focused on areas used by the majority of the herds. Three to six pellet groups were collected at each site. The mean (±SD) number of pellet groups analysed per herd was 46.1±20.2 (range 14-88). The location of the site was marked on a map at 1:200,000 scale. With a few exceptions these feeding sites were located far from sites where supplemental foods were provided. Two slides were investigated for each pellet group, and the relative density for each forage type was calculated. We pooled data over October-December and January-March and related the herd means of five main components - ground lichens *Cladonia, Stereocaulon, Cetraria*, dwarf-shrubs *Vaccinium, Empetrum, Ledum, Calluna*, grasses *Graminae*, sedges *Cyperaceae* and mosses *Dicranum, Polytrichum, Pleurozium* - to the biomass of ground lichens. Data from October-December were available for 12 herds only. Because reindeer fed in the same areas throughout the winter, we related diet composition to the herd's mean lichen biomass pooled over all feeding sites.

Lichen biomass

Lichen biomass was assessed at 201 actual winter feeding sites in 1991. In herds from which faecal pellets were collected, the sites (n = 174) were the same as those where faecal material was collected. The mean (±SD) number of these sites per herd was 12.3 (±7.1) and the range from 6 to 28. Herd explained for 53.1% of the variation in lichen biomass at feeding sites (oneway ANOVA, $F = 10.19$, $df = 13, 187$, $P < 0.001$). The percent coverage and height of lichens were assessed from 10 to 15 quadrats of 0.25 m^2 located along a line at a distance of 10 m from each other. The location of the first quadrat was selected at random. Dry matter (DM)/ha figures for lichens were calculated according to the functions provided by Mattila (1981).

Supplemental feeding

The natural diet of 10 herds was supplemented with dry hay in February and March. Figures for the annual amounts of hay supplied per reindeer (2-29 kg) were collected from the annual reports of each herding association.

Density

Reindeer were counted in roundups held in October-January. Density was calculated for the area suitable for lichen growth (Mattila 1981). The annual variation in the accuracy of the counts was small (Helle & Kojola 1993). Both density and reproductive rates increased from 1974 to 1987 (Helle & Kojola 1993, Kojola & Helle 1993), but evident signs of density-dependent food limitation began to appear in 1988. Density-dependent reproduction and

the effect of lichen biomass on reproduction were analysed using means for the period 1988-1992.

Body weight

Fully dressed carcass weight, equivalent to live weight minus head, skin, viscera, blood and metabodials (Langvatn 1977), was used. The sex, cohort (calf-adult) and dressed body weight of each slaughtered reindeer were recorded in a »selling book«. We selected the body weights of 100 calves and does at random from animals slaughtered between 15 November and 15 December in 1991; with a few exceptions slaughtered does were older than 3 years.

Statistical analysis

We used herd means in statistical treatments. Arcsin transformed square roots were calculated for the proportion of each forage type in diet, calf/doe ratios and the coefficient of variation (CV) of the calf/doe ratios (see Ranta et al. 1989). Linear relationships were obtained through log-transformations of lichen biomasses; and simple linear regressions were performed to measure the density-dependent calf/doe ratio, the effect of lichen biomass on the proportion of different forage types, the calf/doe ratio and the CV of calf/doe ratio. The adjusted r-square, correlation and probability are reported for each regression. All the reported probabilities are two-tailed.

Results

Diet composition

Pooled over herds, the proportion of various plant groups for the entire winter decreased in the order lichens, dwarf shrubs, mosses, sedges and grasses. Lichen biomass affected the proportions of dietary lichens and dwarf shrubs in both early and late winter. Our results suggest that lichens were the predominant forage when lichen availability was higher than average (Fig. 2). Dwarf shrubs con-

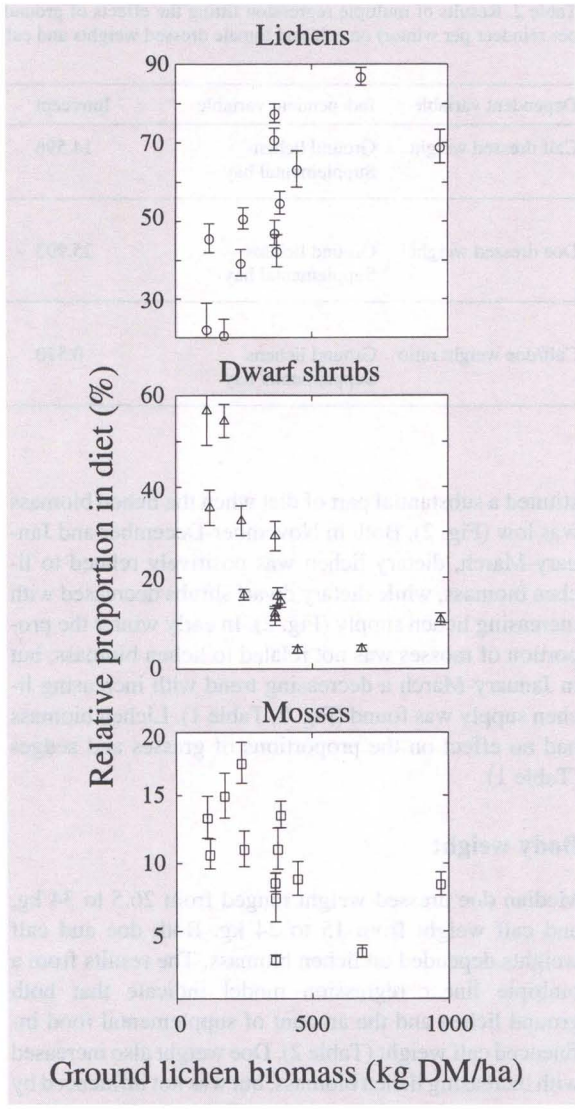

Figure 2. The relationship between mean lichen biomasses (kg DM/ha) and the diet composition (herd mean ±SE) in January-March.

Table 1. Proportion of main winter forage components in faeces and results of linear regression fitting arcsin-transformed square roots of proportions of dietary lichens, dwarf shrubs and mosses to lichen biomass at winter feeding sites of reindeer.

Period	Forage	Proportion in diet (% mean±SD)	Adjusted r^2	Correlation r	n	p
Nov.-Dec.	Lichens	53.9 ± 18.6	0.301	0.604	12	0.038
	Dwarf shrubs	16.5 ± 16.6	0.621	-0.809	12	0.001
	Mosses	7.8 ± 4.3	0.000	-0.192	12	0.549
	Grasses	2.3 ± 1.8	0.000	-0.075	12	0.816
	Sedges	7.8 ± 4.8	0.000	-0.058	12	0.858
Jan.-Mar.	Lichens	53.2 ± 20.1	0.543	0.762	13	0.002
	Dwarf shrubs	22.9 ± 17.5	0.644	- 0.821	13	0.001
	Mosses	10.7 ± 4.3	0.185	- 0.503	13	0.080
	Grasses	3.1 ± 2.6	0.106	- 0.425	13	0.148
	Sedges	3.2 ± 2.2	0.000	- 0.047	13	0.879

Table 2. Results of multiple regression fitting the effects of ground lichen biomass at feeding sites (kg DM/ha) and supplemental hay (kg per reindeer per winter) on calf and female dressed weights and calf/female weight ratio in 1991.

Dependent variable	Independent variable	Intercept	Coefficient	t	P
Calf dressed weight	Ground lichens	14.596	0.007	3.629	0.004
	Supplemental hay		0.021	2.453	0.034
			$F = 7.292$, $r^2 = 0.492$, $n = 14$, $p = 0.010$		
Doe dressed weight	Ground lichens	25.993	0.006	3.281	0.020
	Supplemental hay		0.021	0.445	0.665
			$F = 5.702$, $r^2 = 0.420$, $n = 14$, $p = 0.020$		
Calf/doe weight ratio	Ground lichens	0.570	0.001	2.494	0.030
	Supplemental hay		0.004	3.506	0.005
			$F = 7.010$, $r^2 = 0.480$, $n = 14$, $p = 0.011$		

stituted a substantial part of diet when the lichen biomass was low (Fig. 2). Both in November-December and January-March, dietary lichen was positively related to lichen biomass, while dietary dwarf shrubs decreased with increasing lichen supply (Fig. 2). In early winter the proportion of mosses was not related to lichen biomass, but in January-March a decreasing trend with increasing lichen supply was found (Fig. 2, Table 1). Lichen biomass had no effect on the proportions of grasses and sedges (Table 1).

Body weight

Median doe dressed weight ranged from 26.5 to 34 kg, and calf weight from 15 to 24 kg. Both doe and calf weights depended on lichen biomass. The results from a multiple linear regression model indicate that both ground lichen and the amount of supplemental food influenced calf weight (Table 2). Doe weight also increased with increasing lichen biomass, but was not influenced by the amount of supplemental hay (Table 2). The calf/doe weight ratio increased with increasing lichen biomass and supplemental hay (Table 2). Neither calf nor doe weight depended on the previous winter's density ($r = -0.472$, the adjusted $r^2 = 0.158$ and $p = 0.079$ for both calf and doe weight). Nor did the calf/doe weight depend on density ($r = -0.241$, $p = 0.387$).

Reproduction

The mean reproductive rate in 1988-1992 was positively related to lichen biomass (Fig. 3). Lichen biomass accounted for 22.9% ($r = 0.537$, $p = 0.048$) of the variation in calves/does ratio. This ratio was inversely related to mean reindeer density ($r = -0.646$, $r^2 = 0.368$, $p = 0.013$). Lichen biomass affected the annual variation in the reproductive rate; the CV for 1988-1992 increased with decreasing lichen biomass ($r = -0.703$, $r^2 = 0.467$, $p = 0.004$).

Discussion

Diet composition

Most methods used for establishing the diets of large herbivores, such as oesophageal fistulation, direct observation and rumen samples, do not usually allow sufficient sample sizes for population-level diet estimation. Faecal analyses, while permitting practically unlimited sampling suffer from some disadvantages (Holechek et al. 1982, Gill et al. 1983). Most important, the results of a faecal analysis to determine food plant composition do not necessarily agree with the actual diets. However, high similarities have also been reported (Casebeer & Koss 1970, Johnson & Pearson 1983). The agreement between microhistological faecal analysis and diet composition has

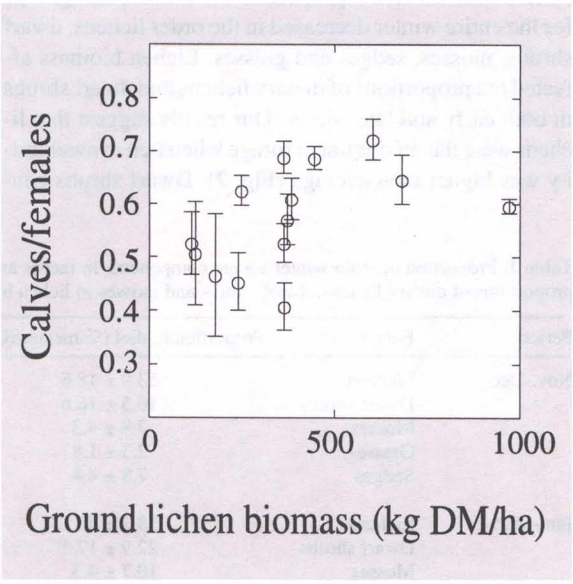

Figure 3. The relationship between mean lichen biomass (kg DM/ha) and calf production (herd mean ±SE).

not been experimentally tested in reindeer. Nevertheless, we have reason to believe that the results of this analysis reflect the dominant features in the winter foraging conditions of reindeer, because the main effects of habitat deterioration on diet composition - increased proportions of vascular plants and mosses - were similar to those reported in studies where rumen samples were used to assess the winter diet of reindeer or caribou (Thomas & Edmonds 1983, Skogland 1984).

When reindeer mostly relied on natural food resources, the most important alternative food in our study area appeared to be dwarf shrubs. In typical winter habitats of reindeer in northern Finland, the standing crop biomass of dwarf shrubs tends to be much higher than that of lichens, mosses, grasses or sedges (M. Niskanen, unpubl. data). The proportion of grasses would be higher for faecal samples collected close to sites where supplemental hay was provided (up to 70%; Kojola et al. 1993). The highest proportions of mosses were attributed to foraging on heavily exploited lichen ranges, but they are probably not actively selected by reindeer (White 1983, Skogland 1984a).

Growth and reproduction

Skogland (1983, 1990) suggested that winter food limitation usually has a stronger influence on reindeer mass than summer food limitations. Summer density of the summer herd has been found to affect reindeer body mass in northern Norway, where reindeer are packed onto peninsulas and islands, and where densities are many times greater than those of our study herds (Movinckel & Prestbakmo 1969). Winter food supply may affect reindeer autumn mass in several ways. Winter food limitation has a diminishing effect on birth mass (Skogland 1984b), to which calf autumn mass is related (Eloranta & Nieminen 1986, Kojola 1993). It also entails a delay in calving time, which reduces the time left to gain mass before winter sets in (Reimers et al. 1983, Skogland 1983). The effect of supplemental food on calf mass showed that even small increments in winter food supply are effective when extra food is available during the most critical period of the year (see also Boutin 1990). In the herds where feeding was most intensive, the amounts of hay supplied covered only 10-20% of the nutritional demands of reindeer during the period when extra food was supplied (February-March).

Our results suggest that winter food supply had a greater influence on the autumn body mass of calves than does. One probable explanation for differences between calves and females is the connection between food supply and calf mortality. Winter food limitation leads to higher newborn mortality (Skogland 1985). This frees some of the breeding females from the current reproductive investment, which is also likely to migitate the effects on adult female size. The finding that supplemental feeding affected calf more than doe weight may be associated with the timing of feeding. The foetus is growing during the times of supplemental feeding, while adult females gain mass in summer.

Our results did not reveal any dependence between body weight and the previous winter's density, probably because the present condition of lichen ranges reflects the past grazing pressures, too (Kojola et al. 1993). The growing annual variability in the calf crop with increased food limitation is evidently due to the strengthened impact of density-independent factors, particularly on variable snow conditions (see Helle & Säntti 1982). The ultimate reason for the increased variance in calf crop is, however, density-dependent food limitation (Skogland 1985). Habitat deterioration appeared to increase the annual variation in habitat carrying capacity.

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