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A hypothesis to explain lichen-*Rangifer* dynamic relationships

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Abstract: A small group of fruticous lichen species, *viz. Cetraria nivalis, Cladonia mitis, C. stellaris,* and *Stereocaulon paschale* forms extensive mats in the most winter habitats of *Rangifer tarandus* populations in Norway. The plant communities accessible for grazing are often found on easily drained, moraine ridges. These lichen species are perennial, lying on the ground while growing slowly at the top. As they decompose they add humus to the top of the soil profile. The lichen mats catch all water from small showers, thus preventing vascular plants from obtaining a more regular water supply. Grazing removs whole plants and gradually makes larger and larger holes in the lichen mats. Wind and water erode the humus, with only coarse gravel remaining. This diminishes the soil water storage capacity. Without grazing, lichens will gradually build a humus layer, which would improve the soil water storage capacity. In time vascular plants then would take the place of the lichens. I propose the hypothesis that by (over-)grazing *Rangifer* improve their winter pastures by making conditions more favourable for lichens than for vascular plants.The fact that lichens are more scarce on habitats with more and regular precipitation, 1) in more oceanic climates, 2) on soils with more silt, and 3) on bird perches with thick peat due to regular fertilising, support this hypothesis.

Key words: *Rangifer,* reindeer, caribou, lichen, grazing, secondary succession.

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Introduction

In today's management of *Rangifer* populations, semi-domestic and wild, the carrying capacity is often linked to the lichen resources (e.g. Gaare & Skogland, 1980) The objective is to balance the population's yearly intake of lichens and damage from trampling of the lichen mat to its annual regrowth. For the Russian reindeer industry, Andreev (1954) recommended a 3-4 year pasture rotation. One year of grazing should be followed by 2-3 years of lichen regrowth. This conservative management practice has not been the rule in the Fennoscandian semi-domestic reindeer ranges. There most of the winter pastures seem to day to be severely overgrazed. In Norway's wild populations this objective is reached by a rigorous control of the hunt in many of the more than 20 separate ranges.

With studies from Norway, I will first show why conservation of the lichen resources is good in the short term. Then I question this practice, and discuss why it may be unwise for long term resource management.

The relationship between lichens and *Rangifer* has been recognised for a long time. Linnaeus (1735) called the lichens they ate during the winter *Lichen rangiferinus,* a group now separated in several species belonging to many genera.

When the lichen pastures are good, *Rangifer* may have an intake of 80% lichens. The mats of fruticose lichens are composed mostly of species belonging to

Alectoria, Cetraria, Cladonia and *Stereocaulon.* In continental and subcontinental arctic, sub-arctic and alpine landscapes, such lichens often dominate on dry and exposed hills and ridges. In the boreal forest, lichens dominate on easily drained soils between the scattered trees in the taiga and on the forest floor in the open pine forest. In the forest, epiphytic lichens, *viz. Alectoria, Bryoria* and *Usnea,* add to the available winter food. The reindeer may survive without lichens, as on Svalbard (Ekern & Kildemo, 1978; Brattbakk, 1985), but commonly lichens dominate on winter range (Gaare, 1968; Gaare & Skogland, 1975; Eriksson *et al.*, 1981; Chernov, 1985). Therefore, throughout their distribution, *Rangifer* populations benefit from the species unique ability to digest lichens well.

The Snøhetta case

The Snøhetta range at 62°N in the mountain ranges of Southern Norway occupies 3300 km², all above the subalpine birch forest. Fig. 1 show that it is one of more than 20 largely isolated wild reindeer populations in southern Norway (Krafft, 1981). The Snøhetta population was estimated to be a few hundred reindeer in the 1930's (Pet Holaker, pers. comm. 1964). By heavy hunting it had been kept low since a protection period in 1901–1905. The war of 1940–1945 provided a partial protection and allowed the population to grow. Table 1 shows the development from 1946. The rapid rise of the population to 8000–12000 in the 1950's, soon depleted the lichen pastures and this was a matter for much concern. A severe reduction hunt followed up to 1969. Apart for a rise to about 3000 heads in 1977-1983 managers have maintained the population at a low 2000 head in order to allow the lichen pastures to recover.

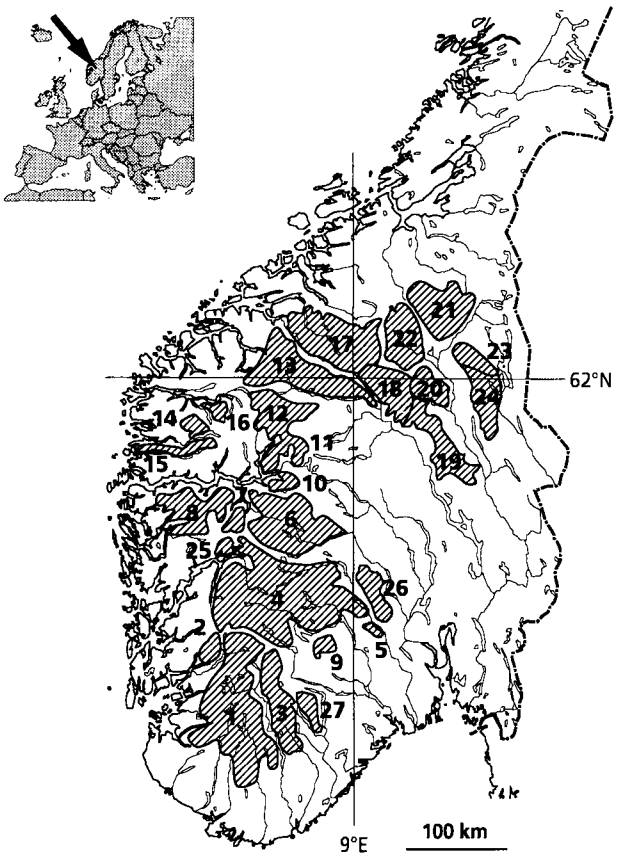

Fig. 1. Wild reindeer ranges in Norway. . Some ranges are small and isolated and marked (*). Ranges where irregular inter migrations are known are grouped: (A) 1 Setesdal Ryfylke, 2* Skaulen-Etnefjell, 3 Setesdal Austhei, 4 Hardangervidda, 5 Blefjell, 6 Nordfjella, 7* Raudafjell, 9 Brattefjell-Vindeggen; (B) 10 Lærdal-Årdal, 11 Vest-Jotunheimen, 12 Ottadalen Sør, 13 Orradalen Nord; (C) 14* Førdefjella, 15* Sunnfjord, 16* Svartebotn; (D) 17 Snøhetta 18 Rondane Nord, 19 Rondane Sør, 20 Sølnkletten, 21 Forelhogna, 22 Knudshø; (E) 23 Tolga østfjell 24 Rendalen. Total area occupied by wild reindeer are 36000 km², total population 38000 (March 1995). The map is redrawn after Krafft (1981).

Railway construction, ending in 1921, divided the range. According to local residents, the small population at that time did not cross the railway along the natural east-west migration route used formerly. But as the population grew, the old migration routes were re-established (Skogland & Mølmen, 1980), despite the railway and a parallel highway. These routes were in regular use every autumn and spring during the period 1957-1983 involving a minimum of 10-50% of the herd. After that, the use of eastern winter ranges became more irregular, and not reported since 1985.

Norway has today few large predators, and hunting has been the dominant mortality factor in all reindeer populations since 1900 (Arild Landa, pers. comm.). In Snøhetta, the annual hunt has been about 367±53 animals over the last 12 years or about 18% of the winter population. The producti-

Table 1. Wild reindeer population in the Snøhetta range, and irs density on the winter lichen pastures. Density is calculated on the basis of the lichen cover in heaths covering ridgetops, mainly *Loiseleurio-Arctostaphylion* (Kalliola, 1939). Such heaths was estimated to 517-634 km² (c.i.) in an aeroplane surway (Gaare, unpubl.). The calculation is based upon official censuses (Norwegian Directorate for Nature Management).

Year	Heads	Heads/km²	(95% conf.int.)
1946	4700	10,0	16,3
1955	12000	25,6	41,5
1960	15000	32,0	51,9
1962	12000	25,6	41,5
1966	6000	12,8	20,7
1969	1200	2,6	4,1
1972–1977	2000	4,3	6,9
1978–1983	3000	6,4	10,4
1984–1995	2000	4,3	6,9

The precipitation is about 300-400 mm/yr in this eastern part of the range. The vegetation on the ridges belongs to the alliance *Loiseleurio-Arctostaphylion* (Kalliola, 1939) with a typical lichen coverage of 65-85%.

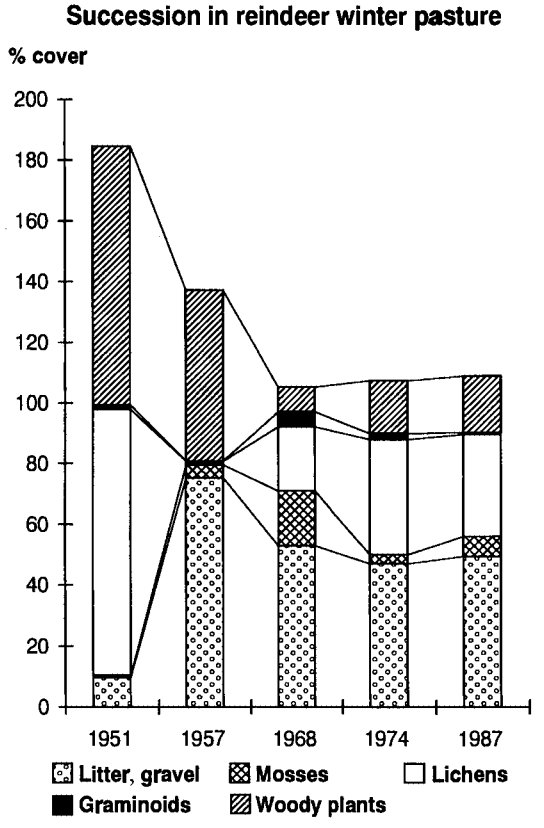

Fig. 2. Recovery of winter pastures in the Snøhetta range after the population high in the 1950's. Data from Nordhagen (1963) for 1951 and 1957 and Gaare (unpubl.) for 1963-1987. The more than 100% coverage in Nordhagens data is in part due to a transformarion from Hult-Sernander scale ro percent coverage.

vity of the herd thus seems to be rather low, confirmed by the annual calf counts in summer (Jordhøy *et al.*, 1996). This population produced an average of about 40 calves per 100 females 2 years and older between 1976-1995 compared with 25 and 70 in other wild reindeer populations in Norway.

Table 1 also shows reindeer density on the winter pasture. The accessible winter pasture is 17.4±5.2% (95% c.i.) of the total area with 13.2% of this belongs to the *Loiseleurio-Arctostaphylion* (Kalliola, 1939) alliance in the low, and 4.2% to *Juncion trifidi* (Kalliola, 1939) in the middle alpine region (Gaare, unpubl. data). For the whole range we have between 517–634 km² (c.i.) of lichen dominated heaths where most grazing occurs. Thus the animal density related to the area of the lichen mats is even greater than the table indicates.

About 14 animals to 1 km² of lichen mat will balance the annual growth of lichens (Gaare & Skogland, 1980). The table show that the densities were much higher in the 1950's, causing overgrazing.

This eastern range was monitored in terms of percent cover of major plant groups from 1951 to 1987 by Nordhagen (1963) and Gaare (unpubl. data).

Fig. 2 represents changes in cover from a representative stand near Nordhagen. When heavy grazing depleted the lichen cover from 75 to 2%, wind and water erosion removed much of the humus layer and only coarse gravel remained. During a period of 7–10 years, mosses and graminoid species increased from 2 to12% cover. This vegetation in turn became the necessary shelter for lichen fragments. Over the next 20 years thereafter the former lichen mat gradually was restored. This observation confirmed what was shown elsewhere in heavily grazed areas: mosses increase first, then graminoids, (Palmer & Rouse, 1945; Andreev 1954; Pegau, 1970).

In other studies commenced in 1963 I found that the grazing had depleted the lichen mats on ridge tops from 1200 to 25 g/m². In the arid environments of such ridges, with rapidly drained soils and low precipitation, a large proportion of the area is

left non vegetated. To keep an optimum annual production available for winter food, it is important not to graze excessively.

Research on lichen mats, (Andreev, 1954; Kärenlampi, 1971; Yarranton, 1975 and Gaare & Skogland, 1980) show a logistic type of growth after disturbance, with an intrinsic growth rate of about 0.20, and a potential maximum biomass of 1200–1500 g/m^2 dry matter at about 30 years, depending on climate and species. The logistic growth form implies that the annual growth at low biomass will be 20%, at middle 10%, and at maximum biomass 0%. Thus a mature lichen mat grows at the top and rots at the base at the same rate. Annual growth is a maximum of 50–70 g/ m^2 at medium biomass of 500–700 g/m^2 (Gaare & Skogland, 1980).

The management of the Snøhetta herd since the early 1960's was based on these findings and interpretations. As a result of the population reduction and subsequent shift in winter grazing to neighbouring ranges, the lichen mats are now restored to medium biomass over large areas.

Long term considerations

Lichens get water from water vapour in air, dew and small showers. A dry lichen mat of 3–5 cm height can catch the water in a shower of 1–3 mm before the soil is wetted. On rapidly drained mineral soils, under a dry climate, and at a certain precipitation regime, this ability make lichens successful competitors with higher plants, which get water only from the soil reservoir. If no grazing occurs, the lichen mat will continue to grow and form litter by rotting at the base. Over time the soil humus content grows and this improves the water storage capacity of the soil, (Andreev, 1954; 1968). At some point, vascular plants get a stable enough water supply to compete successfully with lichens for light. The relative abundance of lichens will then decline, the highly palatable reindeer food is replaced in winter by dry graminoids and dwarf shrubs, both of lower digestibility.

The long term monitoring necessary to document this has not been conducted anywhere. I will draw attention to three relations that support this hypothesis. A more steady supply of water for vascular plants may happen if 1) the amount of precipitation increases and becomes more regular, 2) the water storage in the mineral soil is improved by increased content of silt and clay, and 3) the water storage is improved by an increased amount of organic content in the soil.

1) The accessible vegetation covering the hills and ridges in areas with poor acid rock show a high, 75% or higher in arid climate, coverage of lichens in the non grazed state (Fig. 2, year 1951). If we move to mote oceanic parts of the range, with annual precipitation of 300 mm, this changes. At 800 mm/year the lichen coverage is down to 50–60%, and at 1200 mm/year it is 20–40% (Gaare, unpubl. data). Instead mosses, graminoids and particularly crowberry (*Empetrum* sp.) increase. Less sunshine and higher air humidity at the coast, adds to this effect. In the coastal lowlands, the comparable vegetation is a *Calluna*-heath with scattered lichens only on the most exposed sites (Dahl, 1987).

2) If we compare ridgetop vegetation in rich and poor soils under the same precipitation regime, we find that lichen dominates more on acid soils. The proportion of silt and clay is larger where the rock is more easily weathered. This improves the soils water storage capacity to the benefit of rooted vascular plants.

3) Also on arid parts of the range, bird perches are found on ridges where the surrounding vegetation is a lichen dominated heath. The perch is occasionally a mire hummock with 30-50 cm deep peat with *Sphagnum* spp., *Eriophorum* sp. and *Rubus chamaemorus.* In its central bottom is a boulder of about 20 cm. This boulder was a resting place and the steady fertilisation by guano has, since the last glaciation (8000 yrs BP) developed the vegetation into mire hummock amidst a dry heath.

All three examples are mainly based on experience from the Norwegian region. They support the hypothesis that when the water storage capacity of the soil on such ridges is improved, the dominance of the fruticose lichens decreases. These pastures will then have smaller amounts of suitable winter food for reindeer maintenance.

A herd of *Rangifer* will increase if the sum of annual hunting and natural mortality are lower than recruitment. This will continue as long as the grazing allows (Klein, 1968) until overgrazing of the lichen mats occurs. If possible, the animals move to other winter areas, if not, natural mortality will reduce their numbers drastically. This allow the

lichen to re-establish as is shown in Snøhetta range. But if we keep the population low, I predict that lichens gradually will decrease in the available winter pastures as humus is added to the soil and water holding capacity increases. They will be replaced by plants with lower digestibility and the reindeer carrying capacity of the range will decrease. To avoid this, the reindeer population should be allowed to overgraze their lichen pastures once every 25 years or so. Consequently, the soil will dry, humus will blow away, some of the vascular plants will die and part of the surface will begin a new successional sequence.

It appears that the dynamic relation between the reindeer population growing at a faster rate than the lichen mats, keeps the secondary succession of the vegetation development after denudation at an early stage. In this stage, lichens dominate on grounds accessible for winter grazing reindeer, a successful coevolution. How general this conclusion is, depends on the climate and soil factors. The structure of the population and the animal grazing behaviour may be equally important. But it is everywhere true that reindeer management should be range oriented, and on a 100-year perspective rather than a 10 year one.

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