Differential effects of reindeer on high Arctic lichens

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Abstract. We studied the effects of Svalbard reindeer on the abundance of lichens in Spitsbergen. A survey was carried out in 14 areas with contrasting reindeer densities. Separate cover estimates for crustose, fructose and foliose lichens were taken in each area, and related to the density of reindeer pellet groups, a measure of reindeer density. Dominant macrolichen families were identified in 10 areas, and a full record of macrolichen species was taken in four additional areas. Variation in reindeer density is partially due to past overhunting, and subsequent incomplete recovery, releasing some areas from reindeer grazing for 100-200 yr.

The cover of fruticose lichens was negatively related to reindeer pellet group density, indicating suppression by Svalbard reindeer. This makes their impact comparable to other members of the *Rangifer* genus around the northern hemisphere. The generally recorded low abundance of lichens in the diet of Svalbard reindeer compared to other *Rangifer* species, therefore, was interpreted as the depletion of fruticose lichens in Spitsbergen, and a subsequent switch to alternative foods.

Of all fruticose lichens, *Stereocaulon* spp. appeared least sensitive to grazing. Crustose and foliose lichen cover was independent of reindeer pellet group density. The cover of crustose lichens was significantly related to latitude, with greater cover in more northern areas. Foliose lichens were more abundant in places where moss cover was high. We conclude that the impact of Svalbard reindeer on lichens is dependent on growth form, with fruticose lichens suffering from grazing, whereas foliose lichens might indirectly benefit from higher densities of reindeer or, like crustose lichens, be controlled by other factors.

Keywords: Fruticose lichen; Grazing impact; Macrolichen; Rangifer.

Nomenclature: Elvebakk & Hertel (1996), except for *Cetraria delisei*, which included both *Cetrariella delisei* and *C. fastigiata.*

Introduction

Members of the genus Rangifer (reindeer and caribou) are dependent on lichens throughout most of their range (Gaare & Skogland 1975; Holleman et al. 1979; Thomas & Hervieux 1986; Danell et al. 1994; Kojola et al. 1998). Lichens are believed to be particularly sensitive to reindeer and caribou as they suffer from both trampling and selective grazing (Pegau 1969; Wielgolaski 1975). This explains the strong impact of these northern herbivores on lichen-dominated systems. For example, the abundance of lichens in the vegetation has been reduced dramatically throughout Fennoscandia, where subsidiary winter feeding allowed reindeer to reach very high densities (Väre et al. 1995; Kumpula et al. 2000). Similarly, unmanaged populations of caribou had a substantial negative effect on the abundance of macrolichens (Thing 1984; Henry & Gunn 1991; Manseau et al. 1996; Arseneault et al. 1997), with particularly dramatic decline reported on islands in the Canadian Arctic where caribou have been introduced (Klein 1987; Ouellet et al. 1993).

In contrast, Svalbard reindeer *Rangifer tarandus platyrhynchus* appear largely independent of lichens and mostly live on mosses and vascular plants instead (Staaland & Punsvik 1980; Staaland et al. 1983; Staaland 1986; van der Wal et al. 2000). It is unknown when reindeer occupied the high Arctic islands of Svalbard, but palynological evidence indicates that reindeer have been resident for at least 5000 yr (van der Knaap 1989). The limited dependence on lichens as food by Svalbard reindeer suggests that thousands of years of reindeer grazing in this extreme and isolated archipelago obliterated macrolichens, forcing Svalbard reindeer to utilize alternative food sources.

We investigated the hypothesis that Svalbard reindeer caused suppression of lichens by measuring lichen cover in 14 areas with contrasting reindeer densities throughout Spitsbergen, the largest island in the Svalbard archipelago. Dominant macrolichen families were identified in 10 areas, and a full record of macrolichen species was taken in an additional four areas. Separate cover estimates of crustose, fructose and foliose lichens were taken in all 14 areas, and related to the local density of reindeer. Variation in reindeer density between areas is largely due to historical factors, as man largely eradicated reindeer in most coastal areas during the 19th century (Wollebæk 1926). Reindeer were protected from 1925, but because of poor accessibility, reindeer did not recolonize the whole of Spitsbergen, which created areas characterised by very low reindeer numbers for 100 or more years (Tyler 1987).

Material and Methods

Data on lichen cover were collected as part of an integrated study on the impact of Svalbard reindeer on high arctic vegetation, which will be published elsewhere. Between 17 July and 24 August 2000, 14 sites across central and northern Spitsbergen were visited (Fig. 1). Sites were selected on the basis of all available information on reindeer numbers in the archipelago, with the

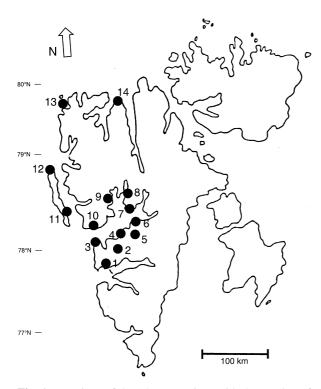


Fig. 1. Locations of the 14 survey sites, with the number of recorded plots in brackets. 1 = Camp Millar (60), 2 = Semmeldalen (60), 3 = Kapp Linné (50), 4 = Bjørndalen (60), 5 = Adventdalen (60), 6 = Vindodden (60), 7 = Skansbukta (60), 8 = Dicksonfjorden (60), 9 = Eckmansfjorden (60), 10 = Tryghamna(60), 11 = Prins Karls Forland-South (40), 12 = Prins Karls Forland-North (18), 13 = Danskøya (20), 14 = Gråhuken (20).

aim of surveying areas with widely differing reindeer densities. At each site, a grid of on average 486 ± 311 m (SD) by 100 m-125 m wide, was set out running from the bottom of a valley up the valley side until plant cover became very patchy. All 10 sites in the Isfjorden and Van Mijenfjorden area (areas 1-10; see Fig. 1) had a grid consisting of $10 \times 6 = 60$ plots except for Kapp Linné with only 50 plots. Four additional sites had lower numbers of plots (18-40 per site; see Fig. 1) due to time and logistic constraints.

In each plot $(1 \text{ m} \times 1 \text{ m})$, a visual estimate of total moss and lichen cover, and separate estimates of crustforming (largely crustose), foliose and bush-forming (fruticose) lichen cover were taken by agreeing cover estimates between two recorders to minimize variation between plots. Samples of the 2-4 dominant macrolichens were collected at sites 1-10. Due to time constraints, we were not able to record the abundance of each lichen species in all survey plot. At sites 11-14, samples of all species of macrolichens within a plot were collected and keyed out under a stereo microscope. No attempt was made to speciate members of Stereocaulon. The few samples for which no positive identification could be made were cross-checked by Eric Steen Hansen (Botanical Museum, University of Copenhagen). Species were classified as either fruticose or foliose lichens following Thomson (1984). As we recorded lichens in 10 out of the 14 sites only as either fruticose, foliose or crustose rather than as species, we are unable to recategorize them. Although this may cause some restrictions upon direct comparison to other lichen surveys, this catagorization is unlikely to substantially alter our conclusions concerning the impact of grazing on lichen abundance in the high Arctic.

Since there are very few recent estimates of reindeer density across Spitsbergen, we used pellet group density as an index of reindeer abundance. This method is commonly used for comparing deer densities between areas (Neff 1968; Putman 1984). All reindeer pellet groups along the full length of the transect within a 2-m wide band were counted. Data were expressed as number of pellet groups per km transect length. Pellets remain visible for many years since their decomposition is very slow. The pellet group counts therefore represent an indication of reindeer density over the last one to two decades.

Cover of lichens was analysed in relation to reindeer pellet group density, latitude and total moss cover, using the PROC GENMOD procedure in SAS version 6.12, employing a log link function and assuming overdispersed Poisson (crustose and foliose lichens) or gamma distribution (fruticose lichens). To avoid pseudo-replication, analyses were run on the average lichen cover for each of the morphological catagories per site.

Results

The cover of fruticose lichens across sites was strongly negatively related to the number of reindeer pellet groups ($F_{1,12} = 10.97$, p < 0.01; Fig. 2), with no significant (p = 0.94) effect of latitude. Average cover of fruticose lichens dropped from 9.4% at low reindeer density to 0.1% at high density. Although visual cover estimates of fruticose lichens for individual plots reached up to 95% in areas with low reindeer density, a maximum of only 1% cover was recorded at the highest reindeer density.

No relationship between crustose lichen cover and reindeer pellet group density was found ($F_{1,12} = 0.33$, p = 0.33). Additional analysis revealed that average cover of this group of lichens across sites significantly increased with latitude ($F_{1,12} = 10.98$, p < 0.01; Fig. 3).

Average cover of foliose lichens across sites was not significantly related to reindeer pellet group density ($F_{1,12} = 2.52$, p > 0.13). However, cover of foliose lichens was positively related to total moss cover ($F_{1,12} = 7.69$, p < 0.02; Fig. 4) with no significant contributions of either reindeer pellet group density (p = 0.49) or latitude (p = 0.87) as explanatory variables.

Prevalence of different dominant groups of macrolichens across 10 survey sites indicated different levels of sensitivity to reindeer density (Table 1). *Stereocaulon* spp. appeared insensitive to grazing, as they were found among the two to four most dominant lichens in nine out of 10 areas. *Cetraria* spp. and, to a lesser extent also *Cladonia* spp. dominated the macrolichen flora only in areas of low reindeer density. The foliose *Peltigera* spp. in contrast were among the dominant macrolichens in areas with intermediate to high densities of reindeer.

Comparison of species specific cover estimates of lichens in four areas with contrasting reindeer densities revealed a similar picture (Table 2). The fruticose lichens *Cetraria delisei*, *C. islandica*, *Cladonia arbuscula*, *C. rangiferina*, *Arctocetraria andrejevii* and *Sphaerophorus globosus* only reached high densities on Prins Karls Forland, where reindeer densities were low. The cover of *Stereocaulon* spp. appeared unrelated to reindeer density. A suite of foliose lichens was found at Gråhuken and Danskøya, mainly *Peltigera* spp. and *Umbilicaria* spp. These species were largely absent from both North and South Prins Karls Forland, areas with low grazing pressure, which could indicate a dependence of these species on reindeer grazing.

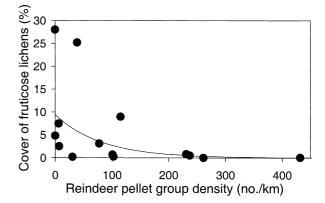


Fig. 2. Average cover of fruticose lichens at sites with contrasting reindeer densities, estimated as pellet group density.

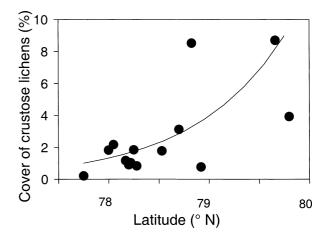


Fig. 3. Average cover of crustose lichens in relation to the latitude of each survey site.

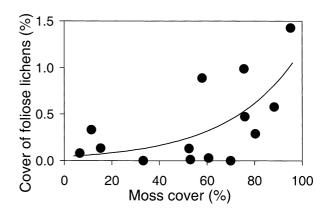


Fig. 4. Average cover of foliose lichens in relation to average moss cover at each survey site.

Table 1. Dominant families of macro lichens at 10 sites across Spitsbergen. Sites are ranked according to reindeer pellet group density (no./km²), an index of reindeer density. Closed symbols indicate families which were among the 2-4 dominant macrolichens. The open symbol indicates that *Cetraria* spp. at Kapp Linné were in extremely poor condition due to grazing. The number in front of each area refers to location in Fig. 1.

Area	Pellet group density	Cetraria	Cladonia	Collema	Nephroma	Peltigera	Pertusaria S	Stereocaul;on
7. Skansbukta	0	•	-	-	-	-	•	•
9. Eckmansfjorden	6	•	•	-	-	•	-	•
8. Dicksonfjorden	7	•		-	-	-	-	•
6. Vindodden	30	-	-	•	-	-	-	•
10. Tryghamna	101	•	•	-	-	•	•	-
5. Adventdalen	102	-	-	-	•	•	•	•
Kapp Linné	115	<<	-	-	-	-	-	•
4. Bjørndalen	237	-	-	-	•	•	-	•
1. Camp Millar	267	-	-	-	-	•	-	•
2. Semmeldalen	432	-	-	-	-	•	-	•

Table 2. Average cover estimates (% ground cover) of individual species of macro lichens for four areas of increasing (left to right)reindeer density, measured as reindeer pellet group density. Cover estimates were averaged over plot recordings in which a particularspecies occurred. Species in bold had an average cover > 1%. Species were classified as either fruticose or foliose lichens followingThomson (1984).

	Prins Karls Forland-South	Prins Karls Forland-North	Gråhuken	Danskøya 13 231 20
Site number on map (Fig. 1)	11 0	12	14 77 20	
Pellet group density (<i>n</i> /km)		39		
Number of plots recorded	40	18		
Fruticose lichens				
Alectoria nigricans		0.3	0.1	
Alectoria ochroleuca		1.1		
Arctocetraria andrejevii		3.0		
Cetraria delisei	22.8	12.9	0.1	0.1
Cetraria islandica	1.2	2.8	0.1	0.1
Cetraria muricata		2.6		
Cladonia arbuscula		22.0		0.6
Cladonia rangiferina	0.7	3.3		
Cladonia spp.	0.6	2.5	0.1	0.1
Flavocetraria cucullata		1.3	0.1	
Flavocetraria nivalis	0.1	0.3	0.1	0.1
Melanelia hepatizon			0.1	
Melanelia stygia			0.6	
Psoroma hypnorum			0.1	
Sphaerophorus fragilis			1.0	
Sphaerophorus globosus	5.0	1.1	0.6	0.1
Stereocaulon spp.	9.5		5.8	7.8
Thamnolia vermicularis		0.2		
Xantoria elegans		0.1	0.1	
Foliose lichens				
Peltigera aphthosa			1.4	
Peltigera leucophlebia				0.1
Peltigera rufescens			0.1	
Peltigera spp.			0.1	0.1
Solorina crocea	0.1			
Umbilicaria arctica			0.1	
Umbilicaria cylindrica			0.1	0.1
Umbilicaria hyperborea			0.5	0.1
Umbilicaria polyphylla	0.1			
Umbilicaria torrefacta				0.1
Umbilicaria virginis				0.1

Discussion

Current patterns of lichen abundance on Spitsbergen are most likely a reflection of historical events and differential response of lichens to reindeer grazing. Historical records from the 17th-19th century, after Willem Barentz (re)discovered Spitsbergen in 1596, indicate that reindeer were widespread throughout the archipelago, and abundant in several places (Wollebæk 1926). Reindeer were hunted throughout the centuries, but from about 1860 onwards, hunting intensity increased dramatically. Modern weapons changed the character of hunting from primarily a subsistence activity, to both a commercial enterprise and a sport (Tyler 1987). Svalbard reindeer were hunted to extinction in most coastal areas, and eventually the species was protected in 1925 to prevent further decline (Wollebæk 1926; Tyler 1987). Recolonization has taken place since, but due to the presence of glaciers this has proved to be a slow process in some parts of Spitsbergen. Lichen growth on Svalbard is also extremely slow (Cooper & Wookey subm.), but in those areas where reindeer grazing pressure has been low for a period of 100-200 yr, fruticose lichens have expanded ion such a way that they form a major vegetation component today. These areas generally appear to be good grazing grounds, and the presence of moss- and lichen-covered antlers indicate former use. We expect that reindeer densities in these areas will eventually increase and transform the vegetation.

Further support for this hypothesis comes from the destruction of fruticose lichens by Svalbard reindeer on Brøggerhalvøya (Ny-Ålesund area), where 15 animals were introduced in 1978, and a sizeable population quickly developed (Aanes et al. 2000). Lichen cover was greatly reduced between 1980 and 1989, and the proportion of mosses in the reindeer diet increased (Staaland et al. 1993). Ongoing research demonstrates that this trend continued and has resulted in a generally depauperate vegetation devoid of macrolichens (Cooper & Wookey subm.). Similarly, we found that continued presence of reindeer on Danskøya (Sysselmannen unpubl.), led to overgrazing and associated soil erosion, with macrolichens only successfully growing when protected from grazing by boulders. Effectively, the patterns observed resemble those on Canadian arctic islands, where introductions of reindeer resulted in overgrazing of the vegetation (Klein 1987; Ouellet et al. 1993). In particular the continued presence of a nonmigratory population of Svalbard reindeer (Tyler & Øritsland 1989) prevents the recovery of grazed vegetation. Currently, Svalbard reindeer are still expanding their range, partly due to migration from their core areas, and partly due to overflow from the introduced population on Brøggerhalvøya (Tyler 1987; Hindrum et al. 1995; J.O. Scheie pers. comm.). There is little doubt that this will eventually lead to a sizeable reduction in fruticose lichens throughout Svalbard. The impact of Svalbard reindeer on fruticose lichens is therefore comparable to other members of the *Rangifer* genus all around the northern hemisphere. The low abundance of lichens in the diet of Svalbard reindeer compared to other *Rangifer* members, therefore, is not likely to reflect a difference in food selection, but a consequence of the depletion of fruticose lichens in the high Arctic systems under study, and a subsequent switch to alternative foods.

In areas where reindeer density was high and consequently the coverage of fruticose lichens typically low, Stereocaulon spp. seemed to be least affected by grazing, as has been found in other systems (Thing 1984). This might be due to reindeer largely avoiding these lichen species due to their low nutritional value (Côté 1998; Svihus & Holand 2000), or possibly to the observation that a moderate level of trampling might be an effective way of distributing propagules. Similarly, the abundance of crustose and foliose lichens appear unrelated to grazing impact. Crustose lichens appear well adapted to high arctic conditions, as their coverage increased with latitude. Foliose lichens were more abundant at places with high moss cover. The moss layer is likely to buffer swings in surface moisture content and therefore foliose lichens might benefit from the association with mosses during periods of drought (Gold & Bliss 1995).

We conclude that the impact of Svalbard reindeer on lichens is dependent on growth form, with fruticose lichens suffering from grazing, whereas foliose lichens might indirectly benefit from higher densities of reindeer or, like crustose lichens, be controlled by other factors.

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References

- Aanes, R., Sæther, B.-E. & Oritsland, N. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography* 23: 437-443.
- Arseneault, D., Villeneuve, N., Boismenu, C., Leblanc, Y. & Deshaye, J. 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Quebec: an application of fire history and Landsat data. *J. Appl. Ecol.* 34: 65-78.
- Côté, S. 1998. In vitro digestibilities of summer forages utilized by the Rivière George caribou herd. *Arctic* 51: 48-54.
- Danell, K., Utsi, P., Palo, T. & Eriksson, O. 1994. Food plant selection by reindeer during winter in relation to plant quality. *Ecography* 17: 153-158.
- Elvebakk, A. & Hertel, H. 1996. Part 6. Lichens. In: Elvebakk, A. & Prestrud, P. (eds.) A catalogue of Svalbard plants, fungi, algae and cyanobacteria, pp. 271-359. Norsk Polarinstitutt, Oslo.
- Gaare, E. & Skogland, T. 1975. Wild reindeer food habits and range use at Hardangervidda. In: Wielgolaski, F. (ed.) *Fennoscandian tundra ecosystems*. Springer Verlag, Berlin.
- Gold, W. & Bliss, L. 1995. Water limitations and plant community development in a polar desert. *Ecology* 76: 1558-1568.
- Henry, G. & Gunn, A. 1991. Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. Arctic 44: 38-42.
- Hindrum, R., Jordhøy, P. & Tyler, N. 1995. Svalbardrein et nøysomt liv på tundraen. *Villreinen*: 105-112.
- Holleman, D., Luick, J. & White, R. 1979. Lichen intake estimates for reindeer and caribou during winter. J. Wildlife Manage. 43: 192-201.
- Klein, D.R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. J. Range Manage. 40: 336-338.
- Kojola, I., Helle, T., Huhta, E. & Niva, A. 1998. Foraging conditions, tooth wear and herbivore body reserves: a study of female reindeer. *Oecologia* 117: 26-30.
- Kumpula, J., Colpaert, A. & Nieminen, M. 2000. Condition, potential recovery rate, and productivity of lichen (*Cladonia* spp.) ranges in the Finnish reindeer management area. *Arctic* 53: 152-160.
- Manseau, M., Huot, J. & Crête, M. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. *J. Ecol.* 84: 503-513.
- Neff, D. J. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. *J. Wildlife Manage*. 32: 597-614.
- Ouellet, J., Heard, D. & Boutin, S. 1993. Range impacts following the introduction of caribou on Southampton Island, Northwest Territories, Canada. *Arctic Alp. Res.* 25: 136-141.
- Pegau, R. 1969. Effect of reindeer trampling and grazing on lichens. J. Range Manage. 23: 95-97.
- Putman, R. J. 1984. Facts from faeces. Mammal Rev. 14: 79-97.
- Staaland, H. 1986. Svalbardreinens ernæring [feeding and nutrition of Svalbard reindeer]. In: Øritsland, N. (ed.)

Svalbardreinen of dens livsgrunnlag, pp. 72-91. Universitetsforlaget, Oslo.

- Staaland, H. & Punsvik, T. 1980. Reindeer grazing on Nord-Austlandet, Svalbard. In: Reimers, E. Gaare, E. & Skjenneberg, S. (eds.) *Proceedings of the 2nd International Reindeer/Caribou symposium, Røros, Norway*, pp. 262-273. Directoratet for vilt og ferskvannsfisk, Trondheim.
- Staaland, H., Brattbakk, I., Ekern, K. & Kildemo, K. 1983. Chemical composition of reindeer forage plants in Svalbard and Norway. *Holarctic Ecol.* 6: 109-122.
- Staaland, H., Scheie, J., Grøndahl, F., Persen, E., Leifseth, A. & Holand, Ø. 1993. The introduction of reindeer to Brøggerhalvøya, Svalbard: grazing preference and effect on vegetation. *Rangifer* 13: 15-19.
- Svihus, B. & Holand, Ø. 2000. Lichen polysaccharides and their relation to reindeer/caribou nutrition. J. Range Manage. 53: 642-648.
- Thing, H. 1984. Feeding ecology of the West Greenland caribou (*Rangifer tarandus groenlandicus*) in the Sisimiut-Kangerlussuaq region. *Dan. Rev. Game Biol.* 12: 1-51.
- Thomas, D. & Hervieux, D. 1986. The late winter diets of barren-ground caribou in North-Central Canada. *Rangifer* Special issue 1: 305-310.
- Thomson, J.W. 1984. American arctic lichens. 1. The Macrolichens. Columbia University Press, New York, NY.
- Tyler, N. 1987. *Natural limitation of the abundance of the high arctic Svalbard reindeer*. University of Cambridge.
- Tyler, N. & Øritsland, N. 1989. Why don't Svalbard reindeer migrate? *Holarctic Ecol.* 12: 369-376.
- van der Knaap, W. 1989. Past vegetation and reindeer on Edgeøya (Spitsbergen) between c. 7900 and c. 3800 bp, studied by means of peat layers and reindeer faecal pellets. *J. Biogeogr.* 16: 379-394.
- van der Wal, R., Irvine, J., Stien, A., Shepherd, N. & Albon, S.D. 2000. Faecal avoidance and the risk of infection by nematodes in a natural population of reindeer. *Oecologia* 124: 19-25.
- Väre, H., Ohtonen, R. & Oksanen, J. 1995. Effects of reindeer grazing on understory vegetation in dry *Pinus sylvestris* forests. J. Veg. Sci. 6: 523-530.
- Wielgolaski, F.E. 1975. Functioning of Fennoscandian tundra ecosystems. In: Wielgolaski, F.E. (ed.) *Fennoscandian tundra ecosystems*, pp. 300-326. Springer-Verlag, Berlin.
- Wollebæk, A. 1926. *The Spitsbergen Reindeer (Rangifer tarandus spetsbergensis)*. Det Norske Videnskaps-Akademi I Oslo, Oslo.

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