Reindeer *(Rangifer tarandus)* and climate change: Importance of winter forage

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Abstract: As a consequence of increasing greenhouse gas concentrations, climate change is predicted to be particularly pronounced, although regionally variable, in the vast arctic, sub-arctic and alpine tundra areas of the northern hemisphere. Here, we review winter foraging conditions for reindeer and caribou (*Rangifer tarandus*) living in these areas, and consider diet, forage quality and distribution, accessibility due to snow variation, and effects of snow condition on reindeer and caribou populations. Finally, we hypothesise how global warming may affect wild mountain reindeer herds in South Norway. Energy-rich lichens often dominate reindeer and caribou diets. The animals also prefer lichens, and their productivity has been shown to be higher on lichen-rich than on lichen-poor ranges. Nevertheless, this energy source appears to be neither sufficient as winter diet for reindeer or caribou (at least for pregnant females) nor necessary. Some reindeer and caribou populations seem to be better adapted to a non-lichen winter diet, *e.g.* by a larger alimentary tract. Shrubs appear to be the most common alternative winter forage, while some grasses appear to represent a good, nutritionally-balanced winter diet. Reindeer/caribou make good use of a wide variety of plants in winter, including dead and dry parts that are digested more than expected based on their fibre content. The diversity of winter forage is probably important for the mineral content of the diet. A lichen-dominated winter diet may be deficient in essential dietary elements, *e.g.* minerals. Sodium in particular may be marginal in inland winter ranges. Our review indicates that most *Rangifer* populations with lichen-dominated winter diets are either periodically or continuously heavily harvested by humans or predators. However, when population size is mainly limited by food, accessible lichen resources are often depleted. Plant studies simulating climatic change indicate that a warmer, wetter climate may cause an altitudinal upward shift in the production of mat-forming lichens in alpine, sub-arctic regions. This is due to an increased potential for lichen growth at high altitudes, combined with increased competition from taller-growing vascular plants at lower altitudes, where the biomass of *Betula nana* in particular will increase. Mat-forming lichens dominant on dry, windblown ridges are easily overgrazed at high reindeer densities. This has long-term effects due to lichens' slow regeneration rate, but may also reduce competition from vascular plants in a long time perspective. Fires may act in a similar way in some forested areas. Accessibility of winter forage depends on plant biomass, snow depth and hardness; ice crusts or exceptionally deep snow may result in starvation and increased animal mortality. Calf recruitment appears to be low and/or highly variable where winter ranges are overgrazed and hard or deep snow is common. Population decline in several *Rangifer tarandus* spp. has been associated with snow-rich winters. Effects tend to be delayed and cumulative, particularly on calves. This is mainly ascribed to feeding conditions for young animals which later affect age at maturation. Global warming may increase the frequency of deep or hard snow on reindeer ranges in Norway, due to increased precipitation and more frequent mild periods in winter. We hypothesise that potential benefits from increased plant productivity due to global warming will be counteracted by shifts in the distribution of preferred lichen forage, reduction of the areas of suitable winter ranges, and generally reduced forage accessibility in winter.

Key words: caribou, climate change, global warming, lichens, snow.

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Introduction

Vast land areas in the Northern Hemisphere are classified as arctic, sub-arctic or alpine tundra. Climate change, a consequence of increasing greenhouse gas concentrations, is predicted to be particularly pronounced, although regionally highly variable. Temperature is in general predicted to increase (Cattle & Crossley, 1995). For most of Scandinavia, it is important to note that most climate change models predict that the bulk of these temperature increases will be in winter, rather than summer (see, for example, references in Ball *et al.*, 1999). Precipitation may also increase (Maxwell, 1992). However, an alternative scenario involving changes in north-south ocean currents predicts a reversed, cooling result concerning the temperature in north-western Europe, after an initial phase of warming. So far, warming appears to be in progress (Crawford *et al.*, 1993). In western Norway precipitation has increased (Førland, 1993). In this paper, we limit our considerations to the expected processes of the initial, warming phase.

In tundra habitats the growing season is short and the standing biomass, production and diversity of plants low. Climate change may have profound effects on plant production and plant communities in these habitats marginal for plant growth, mainly due to changes in the length of the growing season, snow cover and breakdown of organic matter. Despite low plant biomass and low plant production, the tundra supports large herbivores, but in low total densities and species numbers compared to temperate, sub-tropic and tropic regions (Klein, 1970). Nevertheless, the gregarious reindeer/caribou (*Rangifer tarandus*) may occur in large numbers and high densities locally.

Reindeer and caribou, like other ungulates in highly seasonal environments at high latitudes, are physiologically adapted to a reduced food intake in winter, and the appetite of the animals is lower in that season than at other times of the year (White *et al.,* 1981; Suttie & Webster, 1998; Tyler *et al.*, 1999). Calves grow rapidly in summer, but lose weight and grow very little during winter (Klein, 1970; Reimers & Ringberg, 1983; Reimers *et al.*, 1983). Milk production in females and weight gain in adults also occurs during summer, when new plant growth has a high nutrient content. The foetus develops during winter, but does not represent a significant energetic demand on the female until the last weeks of pregnancy (Roine *et al.*, 1982; Adamczewski *et al.*, 1993). Consequently, protein requirements are generally lower in winter than in summer. However, malnutrition and poor body condition during late pregnancy was shown both experimentally (Espmark, 1980; Rognmo *et al.,* 1983) and in studies of wild populations (Skogland, 1984a; 1985a; 1986a) to increase the mortality of newly-born reindeer calves.

In this paper we focus on winter. Two factors determine winter food resources for reindeer: first, the standing biomass of live and dead plant material, and secondly (and perhaps more importantly — at least at some times and at some locations) the accessibility of forage due to snow conditions.

Klein (1967; 1970) hypothesised that the quality and quantity of accessible winter forage determine the reindeer population size that can be supported on a range. Skogland (1985a; b; 1990) claimed that winter forage was more important than summer forage in determining survival of calves, as well as timing of births (which determined the time left for the calves' growth during summer, and potentially their subsequent adult size). On the other hand, the relative importance of summer and winter forage in determining adult size and reproductive success is disputed and may vary among ranges (Reimers, 1983b; White, 1983; Skogland, 1985a; Crete *et al.*, 1990; Couturier *et al.*, 1990; Crête & Hout, 1993; Bergerud, 1996; Ouellet *et al.*, 1997; Heggberget, 1998; Post & Klein, 1999). Nevertheless, winter appears to be the season when forage is most usually restricted, although some exceptions have been demonstrated, *e.g.* the George River herd (Couturier *et al.*, 1990; Crete *et al.*, 1990).

We review factors that determine winter diet, nutrition and foraging conditions for reindeer and caribou, focusing on mountain reindeer (*R. t. tarandus*), and hypothesise how climate change may affect winter foraging conditions for the important populations of wild mountain reindeer in South Norway.

Quality and distribution of reindeer and caribou winter forage

Reindeer and caribou have been classified as grazers/browsers (White *et al.*, 1981) that are intermediate between roughage feeders and concentrate selectors (Hofmann, 1989). They include a rather wide variety of plant species and growth forms in their diet (Bergerud, 1972; White *et al.*, 1981; Skogland, 1984b). In contrast to a carnivorous diet, a plant diet is characterised by a highly variable composition of nutrients and content of digestible energy, depending mainly on plant species, phenological stage and season (Garmo, 1986). While the phenological stage of plant growth is very important for forage quality in summer (Staaland &

Sæbø, 1993, Van der Wal *et al.*, 2000, Walsh *et al.*, 1997) the quality of winter forage varies instead mostly by plant species composition in the diet. It is important to note that most, if not all, of the various methods used to assess the diet of wild ruminants yield biased proportions of forage types, for several reasons that will not be discussed here (see *e.g.* Gaare *et al.*, 1977). Furthermore, although the sample size in such studies tends to be small, Table 1 still provides a reasonable indication of the importance of different plant groups in the diet.

Reindeer and caribou diets in winter

In many reindeer and caribou populations lichens are the dominant food source in winter, often constituting more than 50% of the forage (Table 1). Also, some lichen genera are preferred and actively selected in winter (Danell *et al.*, 1994; Rominger *et al.*, 1996), indicating a high palatability. When lichens are abundant, reindeer and caribou may have an intake of more than 80% lichens, as shown in Fig. 1 which is based on studies from Norwegian ranges with varying lichen biomass (see also Table 1).

Even if lichens may completely dominate the diet, they appear to be insufficient as forage. Neonatal calf mortality among captive female reindeer fed *ad lib.* but exclusively on lichens in late pregnancy was 28% compared to 7% among females receiving a more nutritious diet (Rognmo *et al.*, 1983). On natural ranges, a pure lichen diet is not likely to occur, as most vascular plants are more resistant to grazing than lichens and will also be available in the winter feeding areas. In accordance with this, all the investigations of reindeer and caribou diets we reviewed did document a significant ingestion of vascular plants (Table 1). Shrubs that are often abundant and accessible on winter ranges appear to be the most common type of non-lichen winter forage. They may be over-represented relative to lichens, but not over graminoids, in rumen and faecal samples (Gaare *et al.*, 1977). The large variation in the proportion of graminoids in diets is related to the accessibility. Both on South Georgia and Kangerlussuaq (Table 1), graminoids were abundant on ground that was frequently free of snow during winter.

When the diet of it populations is viewed across the world distribution it is apparent that the species has a wide dietary adaptability depending on what forage types dominate the specific habitats in which they live, the physiological and energetic constraints of winter conditions, and the costs of accessing the forage. Populations of reindeer and caribou exist in areas with little or no lichens, and diets are sometimes dominated by vascular plants (Table 1). In such cases, shrubs, graminoids and herbs are important. On Svalbard and some of the arctic Canadian islands, mosses are also frequently eaten. A native grass *Poa flabellata*, supplemented with less than 10% sea-weeds (Table 1), constituted the winter forage of introduced reindeer on South Georgia, where lichens are scarce (Leader-Williams *et al.*, 1981). The arctic subspecies of reindeer and caribou, Peary caribou (*R. t. peary*) on arctic Canadian islands and Svalbard reindeer (*R. t. platyrhynchus*) also live in habitats with little lichens (Brattbakk, 1985; Adamczewski *et al.*, 1988) and feed on a variety of vascular plant material (Table 1). However, these arctic subspecies appear to have improved fat storage capacities and behaviour patterns that allow summer intake to assist in meeting winter nutrient requirements to a larger extent than in the sub-arctic and alpine subspecies. Also, the alimentary tract of Svalbard reindeer is relatively larger than in Norwegian mainland reindeer, particularly in winter, and thus able to adapt to a coarser diet (Mathiesen *et al.*, 2000; Staaland & White 1991). Even so, the main distribution of the genus *Rangifer* (Banfield, 1961) falls well within the distribution of a few fruticose lichen species of the genuses *Alectoria, Cetraria, Cladonia* and *Flavocetraria*. In favourable winter grounds for *Rangifer* these species dominates the field layer in the vegetation giving the landscape a grey-yellow tinge (Ahti, 1959; Ahti, 1961; Kärnefelt, 1979)

Despite the diversity of reindeer and caribou diets, experiences from reindeer herding suggest that more animals and a higher productivity can be maintained on lichen-rich than on lichen-poor ranges (Helle & Säntti, 1982; Kojola *et al.*, 1995). Winter diets were often dominated by lichens (Table 1) in situations where reindeer or caribou populations were either periodically or continuously heavily harvested by humans (Hardangervidda in Norway) or predators (North American mainland). However, if predation and hunting is minor, as on many of the arctic islands (so that reindeer population size appears to be mainly limited by food), accessible lichen recourses often become depleted.

Chemical composition and digestibility of forage plant species and forms in winter

Studies of the chemical composition of plants eaten by reindeer or caribou have shown that the winter diet tends to have more energy-rich, relatively easily-digestible types of carbohydrates (hemicellulose and to a lesser extent, cellulose), but less protein than the summer forage. This is partly because the

Table 1. Reindeer and caribou winter forage composition (%), given as mean or range. Studies are arranged according to increasing lichen proportions in the diet.

Locality *Rangifer* subsp.	Season	Lichens	Shrubs	Mosses	Graminoids	Other	Analysis method	*n*	Source
South Georgia *tarandus*	Winter				> 90	< 10	Rumen, point count		Leader-Williams *et al.*, 1981
Banks Island *peary*	Nov – Apr	<1	≤ 20		20 - 40	≤ 90	Faeces	6-18	Larter & Nagy, 1997
Svalbard *platyrhynchus*	Winter	<1	7	22	32	41	Rumen, point count	10	Calculated from Sørmo *et al.*, 1999
Svalbard *platyrhynchus*	Apr	2	51	25	Included in “other”	22	Rumen		Staaland *et al.*, 1983
Kangerlussuaq, *groenlandicus*	Oct – Apr	> 6	> 10		58	>5	Rumen, cover	10	Thing, 1984
Finnmarksvidda *tarandus*	Feb	13	16	10	62		Rumen, point count	9	Mathiesen *et al.*, 2000a
Can. arctic isl. *peary*	Winter	2-15	0-10	13-58	15-57	1-42	Rumen, cover	9-53	Thomas & Edmonds, 1983
Ikardulik, *groenlandicus*	Feb – Apr	22	little		13	> 60	Rumen, cover	18	Thing, 1984
Finnmarksvidda *tarandus*	Mar	26	17	7	51		Rumen, point count	9	Mathiesen *et al.*, 2000a
Hardangervidda, *tarandus*	Apr	34	22	12	22	9	Rumen, point count	12	Gaare & Skogland, 1975
Finnmarksvidda *tarandus*	Winter	35	36	6	21	<1	Rumen, point count	11	Mathiesen *et al.*, 1999
Northwest Territ. *groenlandicus*	Oct – Apr	52	26	4	1	17	Rumen, weight	4	Scotter, 1967
Hardangervidda *tarandus*	Dec	53	12	3	26	5	Rumen, point count	13	Gaare & Skogland, 1975
Finland *tarandus*	Jan – Feb	53	23	11	6		Faeces, rel. density	13	Kojola *et al.*, 1995
Finland *tarandus*	Nov – Dec	54	17	8	10		Faeces, rel. density	12	Kojola *et al.*, 1995
Manitoba *groenlandicus*	Oct – Apr	55	22	2	4	17	Rumen, weight	6	Scotter, 1967

Hardangervidda *tarandus*	Jan	56	9	3	27	4	Rumen, point count	9	Gaare & Skogland, 1975
Newfoundland *caribou*	Winter	56*	26	6	7	5	Rumen	8	Bergerud, 1972
Denali Alaska *granti*	Nov – May	62	8	10	11	8	Faeces, rel. density	10	Boertje, 1984
NWT & Saskat. *groenlandicus*	March	69	6	5		21	Rumen, point count	104	Thomas & Hervieux, 1986
Saskatchewan *groenlandicus*	Oct – Apr	73	11	2	1	13	Rumen, weight	10	Scotter, 1967
British Columbia *caribou*	Early winter	9-84*	1?-65			14-35	Faeces, cover count	20-25	Rominger & Oldemeyer, 1990

* Mainly arboreal lichens.

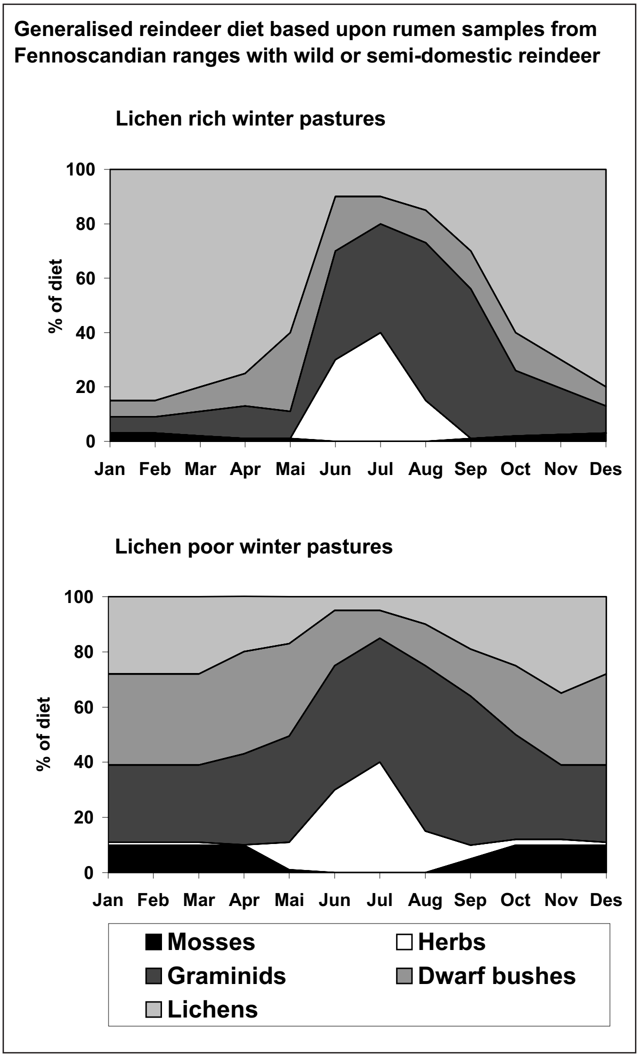

Fig. 1. Reindeer diet estimated for lichen rich and lichen poor ranges. The winter diet is based upon rumen analyses from the following ranges and sources: Snøhetta (Gaare, 1968), Hardangervidda (Gaare & Skogland, 1975), Rondane, Forelhogna and Finnmarksvidda (Gaare, unpubl.). The summer diet is estimated from data by Gaare & Skogland (1975), Skjenneberg *et al.* (1975), Eriksson *et al.* (1981).

proportion of carbohydrates in plants tends to increase from summer to winter, while protein decreases (Staaland & Olesen, 1992), and partly because the selection of plants changes in favour of more energy-rich forage species (Klein, 1990). This is in accordance with the seasonally-differing physiological needs of the animals. Table 2 is compiled from several studies where the plant material for analysis was collected in winter, and compares the content of protein and carbohydrates and gives digestibility for forage types. Concerning chemical composition, Table 2 includes only analyses where comparable information on carbohydrates was given or could be recalculated from the data provided, with one exception: that of *Poa flabellata*. Its total dominance of the winter diet on South Georgia made it interesting enough to include in spite of the sparse information on its nutrient composition.

Lichens in particular are rich in digestible carbohydrates, but low in protein (Table 2). Some graminoids are also relatively energy rich, but tend to be low in protein in winter. Shrubs and mosses in general have higher protein contents in winter than both lichens and graminoids (that are mostly available as litter and standing dead parts), but the grass *Poa flabellata* on South Georgia was found to have a relatively high protein content.

The diversity of winter forage is probably important for the mineral content of the diet. Lichens are low in essential macro-mineral content (Staaland & Hove, 2000), which potentially may restrict calf growth (McDowell, 1992). Dietary sodium supply in inland areas may be marginal, particularly in the winter diet, as demonstrated by Staaland & Hove (2000) for a reindeer herd in South Norway.

Reindeer/caribou is one the few herbivore species that have been shown to digest lichens well (Rominger *et al.*, 1996; Suttie & Webster, 1998). Comparison within and among studies (Table 2) shows that they were able to digest more than 50% of the dry matter of the most important lichen species. For *Bryoria* sp. (an arboreal lichen) as much as 88% was digested *in vitro*. Differences between *Rangifer tarandus* ssp. also appear to exist: for example Svalbard reindeer have been shown to be physiologically and anatomically adapted to digest mosses and other fibrous vascular plans better in winter than reindeer from the Norwegian mainland (Staaland *et al.,* 1979; 1983; Staaland & White, 1991; Mathiesen *et al.*, 2000b).

Digestibility is difficult to measure directly and various experimental methods which do not yield entirely comparable results have been used to estimate digestibility of plant species and plant parts for reindeer and caribou. Interestingly, while winter green plants appeared to be more digestible than non-green plant material when digested *in vitro*, this difference largely disappeared when digested *in vivo*. Even dead and dry plants were digested more than 50%, although the variability (not included in Table 2 in the interests of brevity)

Table 2. Protein and carbohydrate composition in winter of reindeer/caribou forage plants in % of dry matter. The following calculations were made when variables in the table were not directly reported in the source: crude protein = N x 6.25 (Staaland *et al.*, 1983); hemicellulose = NDF - ADF; cellulose = ADF – ADL; (Heiskar & Nieminen, 1988); where NDF= neutral detergent fiber (=cell wall), ADF = acid detergent fiber, ADL = acid detergent lignin. Digestibility figures in parenthesis were obtained with inoculum from sheep.

Locality Taxon/plant group	Crude protein	Hemi-cellulose	Cellu-lose	Lignin	Digestibility In vitro	 In vivo	Source
West Greenland							Staaland & Olesen, 1992
Graminoids:							
Kobresia myosuroides	4.4	34.1	31.0	2.8	(59.7)		
Calamagrostis langsdorfii	2.5	38.1	39.1	2.5	(46.3)		
Pooled monocots	4.4	34.7	28.8	2.9			
Betula nana	7.5	10.8	15.2	22.2			
Salix glauca	10.6	10.7	17.8	13.4			
Mosses	11.3	27.4	27.2	6.5			

Circumpolar							Klein, 1990
Evergreen	8.1	20.6	25.5	13.7	42.5	57.6	
Early winter green	9.6	12.9	23.5	15.0	36.7	40.4	
Early winter other	6.9	25.1	22.4	7.4	30.8	53.4	
Mid/late winter green	11.5	24.0	27.3	5.8	52.7	59.6	
Dead/dry	7.3	21.6	25.9	7.9	28.8	51.0	
Hippuris vulgaris	14.2	4.7	19.6	12.0	43.1	67.8	
Muskrat pushups	19.9	14.4	31.5	9.3	39.1	47.4	
South Georgia							Leader-Williams *et al.*, 1981
Graminoid:							
Poa flabellata	7 – 9.5						
Finland							Heiskari & Nieminen, 1988
Lichens					37.8	53 - 75	
Graminoids:							
Deschampsia flexuosa					69.8		
D. flexuosa cured leaves					41.2		
Dried grasses and sedges					51.4		
			Cellulose	lignin			
Northern Sweden							Danell *et al.*, 1994
Lichens:							
Bryoria sp.	5.1	32	4		88		
Cladonia arbuscula	3.2	70	6		57		
C. rangiferina	3.7	72	6		69		
C. stellaris	3.3	71	5		41		
Stereocaulon paschale	5.4	59	10		36		
Moss:							
Pleurozium schreberi	4.9	39	40		20		
Dwarf shrubs:							
Empetrum hermaphroditum	6.2	10	27		41		
Vaccinium myrtillus	6.0	23	44		27		
Graminoid:							
Deschampsia flexuosa	7.0	28	25		79		
Northwest USA							Rominger *et al.*, 1996
Lichens							
Bryoria spp. + *Alectoria* sp.						82	

was particularly high for this category. These results indicate that reindeer and caribou can make good use of some types of plant litter, which in winter tend to yield more protein but less energy than lichens. In all cases where *in vitro* and *in vivo* experiments were compared, the *in vivo* digestion was higher for all forage types. Due to the high lignin content of woody plants in winter, shrubs may be expected to have a relatively low digestibility, and this is indicated by some of the *in vitro* studies reviewed in Table 2. However, apparent differences between lignified and other forage types from *in vitro* experiments tended to cancel out when experiments were carried out *in vivo*, so free-ranging animals might digest shrubs more efficiently than expected.

Some graminoids appear to represent good, balanced winter forage, containing more protein than the lichens and more carbohydrates than the shrubs. Judging by the *in vitro* studies (Table 2) they are at least as digestible as the lichens and more digestible than the shrubs. Female semi-domestic reindeer from North Norway maintained their body weight in winter on a diet dominated by graminoids (Mathiesen *et al.*, 2000a). For wild reindeer on alpine tundra in Norway, the most easily-accessible graminoids on the winter ranges are likely to be *Festuca ovina* and *Juncus trifidus* which grow on exposed ridges. Their forage qualities in winter are not known to us. However, graminoids only constituted 4-6% of the lichen-dominated diet at Hardangervidda in the 1970s (Table 1). Lichens, having higher digestibility and a higher available energy than virtually all vascular plant parts in winter, are very important as an energy source in the winter diet. Lichens may also be available in higher density than vascular forage plants on arid moraine soils.

Impact of climatic change on sub-arctic and arctic vegetation

Increasing temperatures, expected as a consequence of global climate change, may produce morphological and phenological responses in tundra vegetation. Examination of polymorphic species on Spitsbergen, Svalbard, indicated that such forms adapt to increased temperatures by changed frequencies of ecotypes, rather than by migration (Crawford *et al.*, 1993). Also, key phenological events such as leaf bud burst and flowering occurred earlier in experimentally-warmed arctic and alpine plots (Arft *et al.*, 1999), indicating that the nutrient content of potential forage would peak earlier in the season (see *e.g.* Chapin *et al.*, 1980; Van der Wal *et al.*, 2000; Walsh *et al.*, 1997).

Sætersdal & Birks (1997) predicted that the direct distributional response of most Norwegian mountain plant species to increasing temperature will not be dramatic, because of their considerable tolerance to variation in mean temperatures. Increased temperature alone was shown to have little effect on arctic plant production even after several growing seasons (Hobbie & Shapin, 1998; Arft *et al.,* 1999). However, the expected climatic change also involves increased precipitation and nutrient availability, so one must be careful in generalizing.

Cooper *et al.* (2001) studied effects of increased summer cloudiness and precipitation on lichen growth. Shading was not found to affect lichen growth, while watering increased growth, particularly in damaged thalli. The authors concluded that the predicted climate change should ameliorate growth conditions for lichens, and help to reduce damage done by reindeer.

Combined effects have been shown in several studies. Chapin & Shaver (1996) simulated climatic change with respect to light, temperature, nutrients and length of the growing season in tussock tundra in northern Alaska. This experiment demonstrated that biomass and turnover rate of the four dominant vascular plant species responded individually to the different treatments, due to individual changes in the rates of production and mortality. The deciduous birch *Betula nana* responded quickly, becoming taller and increasing from an initial 36% to 90% of the total vascular plant biomass after 9 years of combined nutrient and temperature treatment. The biomass of the graminoid *Eriophorum vaginatum* doubled after 9 years in the temperature treatment, but was reduced when temperature and nutrient treatments were combined, due to increased mortality. The biomass of the evergreen dwarf shrubs *Ledum palustre* and *Vaccinium vitis-idaea* responded more slowly to the treatments, but tended to increase with temperature and decrease with nutrients. The nitrogen and phosphorus content of plant shoots increased after treatment in evergreen shrubs and in the graminoid, thus their quality as forage increased, at least in summer. These nutrients tended to decrease in temperature-treated *Betula nana*. As a result, in a climate-changed future *Betula nana* would be highly available, but less nutritious — potentially a very important change regarding the economically-important reindeer in Scandinavia.

The indirect effect of the timing of snowmelt on food availability and quality in subsequent winters is unclear, but Van der Wal *et al.* (2000) did not find significant differences in the shoot density at the end of the growing season just before the onset of winter in *Luzula confusa* or *Salix polaris*.

In two studies of the responses of sub-arctic plant communities in northern Sweden to simulated climatic change (Molau & Alatalo, 1998; Press *et al.*, 1998) lichens responded differently, depending on plant community type. In a dwarf shrub heath in open birch forest at 400 m a.s.l., lichen biomass was reduced on temperature- and nutrient-increased plots to 56% and 18% of control plots respectively (Press *et al.*, 1998). In this plant community, the grass *Calamagrostis lapponica* increased dramatically after nutrient addition, the canopy height increased due to both temperature and nutrient increase, and the biomass of the dominant dwarf shrubs increased in response to temperature, while their abundance was unaffected. In contrast, the lichen cover in both a rich meadow and a poor heath at 1000 m a.s.l. increased in response to both temperature and fertiliser (Molau & Alatalo, 1998). Temperature enhancement increased bottom layer cover in the rich meadow, but diversity was reduced, while in the poor heath both cover and diversity decreased (Molau & Alatalo, 1998). Biomass (Press *et al.*, 1998) and cover (Molau & Alatalo, 1998) of mosses was reduced when nutrients were added. Molau & Alatalo (1998) pointed out that abundant vascular plants might constrain the responses of non-vascular plants. In the study areas compared here the canopy height was also largest and increasing in the dwarf shrub heath, which may have inhibited the lichen growth. Thus, the differing responses of lichens in these studies were possibly the result of differing competition from vascular plants.

Effects of grazing on lichen biomass and composition of winter forage

The temporal quality and distribution of forage types can be determined by factors other than climatic, edaphic and light conditions. Grazing in itself often exerts a strong influence on the realised vegetation type and composition. Vascular plants in general tolerate grazing well, as many of them regenerate complete above-ground parts, or a large proportion, each growing season, and may even overcompensate for the biomass removed by grazing (Post & Klein, 1996; Wegener & Odasz, 1997). In contrast, mat-forming lichens are particularly susceptible to grazing depletion because of their loose attachment to the substrate and because the whole thallus (which may represent accumulated growth over several decades) is eaten. On Southampton Island, Canada, where caribou were re-introduced, lichen biomass was significantly reduced from one year to the next (Ouellet *et al.*, 1993). Following re-introduction of Svalbard reindeer on the Brøgger peninsula at Svalbard, the preferred lichen species was practically eliminated within 9 years (Staaland *et al.*, 1993). Excluding reindeer from plots on the Brøgger peninsula at Svalbard increased both the number of lichen species and percentage cover, suggesting their ability to completely alter lichen community structure both by trampling and selective feeding (Cooper & Wookey 2001). The recent history of the Snøhetta reindeer range in Norway, at 62°N, above the subalpine forest, may illustrate the relationship between reindeer and lichen pastures. This is based on measurements of reindeer winter forage since 1951 (Nordhagen, 1963; Gaare, 1997) and information on population sizes dating back to the 1930s (Gaare, 1997). The Snøhetta population was estimated at a few hundred reindeer in the 1930s, and was kept low by heavy hunting. During the Second World War, hunting was much reduced, which allowed the population to increase (Fig. 2). A rapid rise in the population (to 8000-12000 reindeer in the 1950s) depleted the lichen pastures. The population was subsequently intentionally reduced by hunting until 1969, and the population has since then been maintained at about 2000 individuals in order to allow the lichen pastures to recover. From 1957 to 1983 some of the reindeer regularly moved out of the Snøhetta range during winter, across a railroad and main road that normally functioned as a barrier to migration (Skogland, 1986b; Gaare, 1997).

About 14 reindeer per km^2 of lichen mat will balance the annual growth of lichens (Gaare & Skogland, 1980). The density of reindeer in the Snøhetta range exceeded 30 animals per km^2 of lichen mat in the 1950s, and resulted in overgrazing. This range was monitored in terms of percent cover of major plant groups from 1951 to 1997 (Nordhagen, 1963; Gaare, 1997; Gaare, unpubl.). Heavy grazing reduced the lichen cover from 75% to 2%. Later, wind and water erosion removed much of the humus layer leaving only coarse gravel on the ridges. During a period of 7-10 years, mosses and graminoids increased from 2% to 12% cover. The increase was first evident for the mosses. Over the next 20 years thereafter the former lichen mat was gradually restored.

Research on lichen mats, (Andreev, 1954; Kärenlampi, 1971; Yarranton, 1975; Gaare & Skogland, 1980) shows a logistic type of increase, with an intrinsic growth rate of about 20%, and a potential maximum biomass of 1200-1500 g/m^2 dry matter about 30 years after disturbance

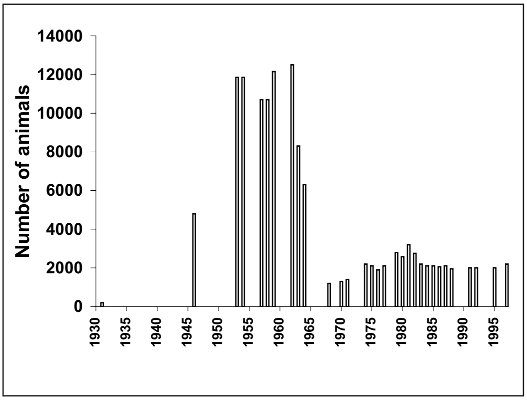

Fig. 2. Wild reindeer winter population estimation in the Snøhetta range, based on Holaker (pers. comm., data for the 1930s), official statistics, and Jordhøy *et al.* (1996).

depending on climate and species. A model calculated by Kumpula *et al.* (2000) shows comparable results for Finnish lichen woodland. The logistic growth form suggests that the annual increase at low biomass will be 20%, at middle 10%, and at maximum biomass 0%. This happens because a mature lichen mat grows at the top and decomposes at the base at the same rate, gradually building up humus. In the arid environments of ridges, with rapidly-drained soils and low precipitation, lichens that absorb water directly from the air have a competitive advantage over vascular plants. This relationship is reversed as the humus layer builds up, trapping water and accumulating nutrients available to vascular plants. In a long-term perspective the mature lichen mat may therefore be succeeded by vascular plants if it is not occasionally destroyed, for example by heavy grazing (Gaare, 1997). Thus, it is interesting to note that both heavy grazing and no grazing may lead to elimination of lichen mats, but in vastly different time perspectives. Fire may have similar effects, particularly in forested areas (Klein, 1982; Arseneault *et al.*, 1997; Hörnberg *et al.*, 1999; Miller, 2000), but wildfire is highly unusual in Norwegian reindeer ranges.

As a result of the reduction of the reindeer population on the Snøhetta range and a subsequent shift in winter grazing to neighbouring ranges (Gaare, 1997), the lichen mats have now been restored to medium biomass over large areas. So far, the variation in the lichen pasture has been explained above as a density-dependent relationship with the reindeer population. However, all changes need not be related to the reindeer population size. Since the reindeer population now has been stable for about 30 years, and the lichen measurements cover a considerable climatic (i.e. east - west) gradient, it should be possible to look for density independent influences like weather as well.

The relatively abrupt depletion of lichen recourses described above were all induced by drastic management initiatives. Inuit knowledge and demographic studies indicate that lichen forage and caribou density on southern Baffin Island cycled in opposite directions over 60-70 years, induced by winter range fidelity of caribou, which was followed by mass emigration and shifting of winter range (Ferguson & Messier, 2000; Ferguson *et al.*, 1998). The time of shift appeared to be predictable from caribou body condition and density.

Distribution of winter forage for reindeer in South Norway

As shown by the diet studies, lichens are the preferred and staple winter food for reindeer when available, and lichens commonly dominate on winter ranges (Gaare, 1968; Gaare & Skogland, 1975; Eriksson *et al.*, 1981; Chernov, 1985). The lichen vegetation that reindeer feed on in South Norway is to a large extent dominated by mat-forming ground lichens, *Cetraria nivalis, C. cucculata, Cladonia arbuscula* ssp. *mitis, C. stellaris, C. rangiferina, Stereocaulon paschale*, and to a lesser extent a few arboreal species, *Alectoria* spp. and *Bryoria* spp. in the boreal forest. Although South Norwegian wild reindeer included significant amounts of vascular plants in their winter diet, lichens were the main constituent of their diet throughout winter.

Precipitation and drainage largely determine the distribution of mat-forming ground lichens. In continental and sub-continental arctic, sub-arctic and alpine landscapes, lichens often dominate on dry and exposed hills and ridges. At 60°N in the alpine region of Norway, lichen cover in heaths on bare-blown ridges with less than 400 mm of precipitation annually is 75-85%, and at 1200 mm annual precipitation 40% and less (Knaben, 1950; Dahl, 1957). In the boreal forest, lichens dominate on well-drained soils on the ground in open forest, and epiphytic lichens add to the available winter food. Precipitation largely increases along east-west gradients in South Norway, although local climate may deviate from the general pattern due to mountain relief. Hence, the more lichen-rich areas are mainly found in eastern parts of the reindeer ranges. There is a lack of information on biomass distribution of non-lichen winter forage.

A combination of snow conditions and lichen distribution, i.e. accessibility of lichens, appear to determine winter ranges of the main herds of wild reindeer (Gaare & Skogland, 1975; Skogland, 1984b; Gaare, 1997). Accordingly, South Norwegian wild reindeer herds tend to winter in the eastern part of their ranges, and the main reindeer winter ranges are dry in summer, and have little snow in winter. However, the population is subdivided in more than 20 more or less isolated subpopulations in South Norway (Krafft, 1981), some of them living in small areas with little opportunity for migration.

Accessibility of forage in winter

Snow is the main factor that determines the accessibility of forage in winter, making the ground forage less available and reducing the feeding rate, depending on snow depth and snow hardness (Skogland, 1978; Rominger *et al.*, 2000). Arboreal forage may become more available when deep, hard snow lifts the animals up towards tree branches (Rominger & Oldemeyer, 1990; Helle & Kojola, 1994; Johnson *et al.*, 2001; Kumpula, 2001). However, most wild mountain reindeer herds in Norway winter in treeless areas at relatively high altitudes, where wind-exposed hills and ridges are usually accessible for grazing in that season (Nellemann, 1996; Nellemann & Thomsen, 1994).

Reindeer cratering, snow depth and snow hardness

Several studies have shown that ground-feeding reindeer choose digging sites with less snow depth and snow hardness than average values within a feeding site when making feeding craters (Skogland, 1978; Helle, 1984; Collins & Smith, 1991; Larter & Nagy, 2001). However, below critical upper limits of snow hardness and depth there seems to be relative thresholds that change with the conditions previously encountered, and with season. Pruitt (1959) observed that groups of caribou that stayed in neighbouring locations with differing snow conditions shifted location after a winter storm that made conditions more difficult. Each group moved to a better location, but some of them settled in areas that had just been vacated by other groups, apparently being content with conditions that others had fled. Skogland (1978) found that the Norwegian reindeer would dig in harder but less deep snow in late winter than in midwinter.

Critical limits for snow digging reported in the literature vary widely (see Pruitt, 1959; Bergerud, 1974; LaPerriere & Lent, 1977; Skogland, 1978; Helle, 1984; Thing, 1984; Adamczewski *et al.*, 1988; Brown & Theberge, 1990), from 50-60 cm depth in loose forest snow (Pruitt, 1959) to almost 3 times this depth in snow with numerous very hard layers (Brown & Theberge, 1990). These differences suggest that digging abilities of reindeer and caribou, and critical limits for digging, are not yet well understood. Both the decision to dig in a location and the decision to stay or leave an area is likely to be based on several factors simultaneously, including stimuli indicating probability of finding forage beneath the snow (Bergerud & Nolan, 1970; Bergerud, 1974; Brown & Theberge, 1990). The snow depth and hardness that these animals will dig through clearly depends on what their alternatives are, and more so than has been considered in most studies on their digging abilities. Different reindeer and caribou subspecies differ greatly in their size and the potential effects on their digging efficiencies should also be considered.

While snow depth measurement is fairly straightforward and comparable among studies, meaningful measurements of snow hardness that can be compared across studies have proved more difficult to obtain. Thus, even though many studies acknowledge the great importance of snow hardness, the comparison of hardness values from different studies is not easy. The two main devices used to measure snow hardness are the penetrometer and the Swiss ramsonde. The penetrometer, which measures force per unit area needed to collapse a snow layer (Klein *et al.*, 1950), has been much used in reindeer and caribou studies. However, it is difficult to standardise how to select snow layers for measurement, and to combine measurements from a column of snow to obtain a meaningful index (*e.g.* Pruitt's (1979) suggestions for such an index related to reindeer cratering activity). The ramsonde (de Quervain, 1950; Ager 1965), that measures the force needed to penetrate vertically a layer of snow, is easier to apply consistently than a penetrometer, and thus allows comparison of results between studies. Although the ramsonde is quite insensitive to hardness of soft snow, it is well suited for cratering studies, as depth, not hardness is the important variable when snow is too soft for the ramsonde. It has been increasingly used in reindeer and caribou studies (*e.g.* Brown & Theberge, 1990; Collins & Smith, 1991; Tucker *et al.*, 1991; Nellemann, 1996). Even so, we suspect that some confusion exists in the literature between two different hardness values that are commonly calculated from the ramsonde measurements (ram hardness and integrated ram hardness). These methodological problems contribute to diverging conclusions on critical limits to reindeer and caribou digging in snow.

Snow conditions and reindeer demography

High winter mortality of caribou and reindeer has been observed on arctic islands and in northern Scandinavia in winters with extreme snow or ice conditions (Klein, 1968; Miller *et al.*, 1977; Gunn *et al.*, 1980; Helle & Säntti, 1982; Reimers, 1982; Reimers, 1983b). Mass mortality or dramatic population declines on the arctic islands inhabited by Peary caribou or Svalbard reindeer has been associated with several centimetres of thick ice layers on the ground or in the snow, and delayed melt-off in spring (Gunn *et al.*, 1980; Reimers, 1982; 1983a). A population crash of introduced reindeer on St. Mathew Island in the Bering Sea apparently occurred during a winter with unusually deep snow, and at a time when heavy reindeer grazing had eliminated the lichens (Klein, 1968). In northern Finland, Helle & Säntti (1982) associated high winter mortality of semi-domestic reindeer with hard ice-crusts in the snow, greater depths of loose snow than usual, and snow cover on the arboreal lichens.

Apart from such catastrophic events following extreme snow conditions and the resulting mass mortality of animals, few studies actually demonstrate a relationship between winter mortality and snow conditions within the more moderate ranges of normal between-year variation. However, several studies indicate such a relationship, and some studies also indicate that winter severity may have negative effects on subsequent calf production. Skogland (1987) found indications of a relationship between recruitment of 1-year-olds and snow conditions in the Setesdal-Ryfylke wild reindeer herd, which is the southernmost sub-population in Norway. Crête & Payette (1990) suggested, among other negative factors, a relationship between warmer winters with increased snowfall and consequently later melt-off in spring, and a caribou population decline in Quebec during the first half of the 20th century. Natality for young caribou females in Denali, Alaska, also declined with increasing late-winter snowfall during the winter prior to breeding (Adams & Dale, 1998). Low spring body condition of females and short summer growing season following severe winters probably reduced ovulation frequency in these young females. Post & Stenseth (1999) demonstrated equivalent responses in abundance of the Sisimiut herd in West Greenland, and in female fecundity of the Hardangervidda reindeer herd in Norway. They argued that weather over several winters may have cumulative effects on ungulates, and that effects of winter weather on early development can persist into adulthood. Population growth rate of Svalbard reindeer on the Brøgger peninsula correlated negatively with winter precipitation, and the effect was stronger at high reindeer densities (Aanes *et al.*, 2000). Calf production in Finnish Lapland correlated negatively with temperature and precipitation in the winter prior to the rut, and positively with temperature in the autumn prior to their birth (Lee *et al.*, 2000).

In South Norway winters are prevalently cool or cold, but not usually extremely cold in areas where wild mountain reindeer live. Snow conditions are usually not extreme and the dramatic death rates that occasionally occur on arctic islands have not been documented in South Norwegian reindeer herds. It is perhaps important to note that the reindeer density is also usually kept at moderate levels by hunting.

Calf production tends to be high in Norwegian wild reindeer herds (Table 3), and the predation pressure is low. However, snow conditions are likely to be among the factors explaining why calf production is generally low in the Setesdal-Ryfylke herd of mountain reindeer, and more variable and occasionally lower among arctic Svalbard reindeer than in other Norwegian reindeer herds (Table 3). Snow conditions on the range of the Setesdal-Ryfylke herd are variable and relatively extreme for South Norway (Johansen *et al.*, 1979). Winter feeding areas are also small compared to the summer ranges in the Setesdal–Ryfylke range. On the arctic islands of Svalbard, ice crust formation is thought to be more extreme and variable than in any other Norwegian reindeer range. Most Svalbard ranges are also heavily grazed. Thus potential winter food is more limited, and availability more variable, than on the other ranges presented in Table 3.

Snow conditions and climate

Factors that can make the snow too hard for reindeer cratering are mechanical disturbance that restructures and packs the snow, and the formation or addition of free water in the snow pack which subsequently freezes. Mechanical hardening is most commonly caused by strong winds in open habitats. Also, mechanical disturbance by agents other than wind can harden the snow. Reindeer cratering and trampling is important in this respect. Pruitt (1959) observed that the same site was not cratered more than twice by caribou in a forest habitat. Wind hardening is a gradual process with a relatively slow increase in snow hardness, often resulting in considerable local variability and little or no snow on lichen ridges. Snow hardening caused by freezing of free water in the snow can result in a more quickly-formed, homogenous and terrain-covering ice crust. Such terrain-covering crusts

Table 3. The range of the between-year variation of calves per 100 female-like animals (females >= 1 year old plus a limited proportion of 1-year-old bull calves, Jordhøy *et al.*, 1996) in summer in some wild reindeer areas in Norway.

Wild reindeer area	Calf rate mean (range)	Time period	No. years with observations
Setesdal - Ryfylke	36 (24 – 47)	1983 – 2000	17
Hardangervidda	47 (36 – 62)	1991 – 2000	10
Rondane north	44 (29 – 64)	1991 – 2000	9
Snøhetta east	39 (28 – 50)	1976 – 2000	24
Knutshø	57 (51 – 68)	1991 – 2000	10
Forelhogna	62 (55 – 67)	1971 – 2000	18
Svalbard	38 (11 – 57)	1991 – 1996	6

Sources: Skogland (1987; 1988), Skogland & Jordhøy (1992), Jordhøy & Skogland (1993; 1994), Jordhøy *et al.* (1995), Jordhøy & Strand (1996; 1997; 1998; 1999; 2000; 2001).

probably create greater problems for reindeer/caribou foraging than wind hardened snow, unless arboreal lichens are available and the crust is sufficiently hard to support reindeer and thus make accessible lichens on branches that were formerly out of reach (Simpson *et al.*, 1985).

Snow depth is determined by snowfall in combination with redistribution, mainly by strong wind, ageing processes in accumulated snow, and melting processes. At high altitudes or latitudes, warmer winters with more precipitation may result in more snow and therefore later melt-off in spring, despite higher spring temperatures.

It seems possible to make some general inferences about snow conditions in specific years from meteorological data, although relationships between meteorological conditions and snow conditions are complex. Forchammer & Boertmann (1993) suggested an ablation index, for the purpose of predicting severity of snow conditions for muskox, based on wind and temperatures above $0^{o}C$ for Northeast Greenland. They did not test their index against snow measurements, and relationships between the index and the development of muskox populations were weak. This might partly be because rainfall, relative air humidity and solar radiation are also important for accumulation of free water in the snow (Hestnes *et al.*, 1994). In addition to wetness of the snow, freezing temperatures following a mild period are also important for hardening of an ice crust. Redistribution and hardening of the snow by strong winds should also be considered, as well as any reduction in snow depths by melt-off. A better understanding of these relationships would be useful when investigating relationships between climate and winter conditions for animals like reindeer.

What effects may global warming have on reindeer winter foraging conditions and populations in Norway?

The plant studies reported suggest that temperature increase alone will have less effect on potential winter forage for reindeer than in combination with increased precipitation and recycling of organic matter. These three factors are, however, likely to occur together on the western reindeer ranges in South Norway. Biomass and canopy height of vascular plants may increase (Press *et al.*, 1998) in localities protected by snow cover during winter. Shifts in plant dominance can be expected to be related more to the relative than the absolute responses of individual species, due to competition for light, nutrients, water and space. Mat-forming lichens may have an upward shift, due to a negative outcome of competition with vascular plants at lower altitudes, and an increased lichen growth at higher altitudes where vascular plants are small and less competitive. Mat-forming lichens may also become less abundant in the oceanic, western parts of the present winter ranges of some of the South Norwegian reindeer herds due to increased precipitation, which deprives the lichens of their competitive advantage over vascular plants in obtaining sufficient moisture in dry or well-drained habitats.

Availability of range for wild reindeer in South Norway is presently affected by development of roads, power lines, tourist resorts and ski trails (Nelleman *et al.*, 2000; Vistnes *et al.*, 2001). Increased winter precipitation may result in increased areas of permanent snow on reindeer summer ranges in the western mountains. If this happens over large areas, summer ranges may shift eastwards into the present winter ranges that are more intensively developed and fragmented, and limited to the east by human-inhabited lowlands and valleys. Herds that are now migratory may thus become more sedentary, and areas of suitable winter ranges can be expected to become reduced by the increasing influence of the ocean on climate. Thus, although total plant productivity in the mountains may increase, carrying capacity for reindeer in winter may decrease, due to a compression of winter range and more continuous range use on more overlapping summer and winter ranges. If these changes happen, reindeer may have to include more vascular plants in their winter diet. Winter habitats may become more marginal, particularly in the southern part of the Scandinavian mountains. However, summer conditions might improve due to increased plant productivity. More summer precipitation and cloudy weather also reduce insect harassment of reindeer (*e.g.* Downes, 1986; Toupin *et al.* 1996).

Stochastic weather events are expected to become more important. Snow depth and snow hardness may then become more variable among years, in which case the foraging conditions will inevitably also become more variable. Effects at the population level, including increased mortality, have occurred in wild Norwegian reindeer populations in extreme years, particularly on Svalbard (Reimers, 1982), but apparently also in the southern herd in Setesdal-Ryfylke (Skogland, 1987). Such extreme winters might also become more common in other Norwegian reindeer areas, because none of them currently have a truly continental climate. Winter survival in Norwegian reindeer herds is then likely to become more variable. Changes in calf production are less predictable, because the relative effects of summer and winter forage on female growth and condition (hence on population reproductive rates) are not yet clear (or are variable). Unless harshness of winters is counteracted by increased plant production and reduced insect harassment in summer, productivity and the harvest potential of the reindeer herds is likely to decline, as indicated by the lower or more variable, calf rates in the Setesdal-Ryfylke herd and on Svalbard. Lee *et al.,* (2000) recently made similar predictions for the semi-domestic reindeer herds in Finland. The South Norwegian reindeer herds exist at present at the southern border of the natural distribution of the species.

Thus, overall, we conclude that climatic warming is not likely to be beneficial to the populations of reindeer in Norway. In this paper we have focused on wild reindeer and caribou herds. However, these predictions also pertain to semi-domestic reindeer herds in Norway, particularly those on the Finnmark plains where the ranges are at present heavily grazed. Because of the economic and cultural importance of reindeer throughout Scandinavia and the rapid rate of climate change which is predicted for this area, we suggest that researchers further consider the potential influence of climate change on reindeer.

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