Effects of weather and snow conditions on reproduction and survival of semi-domesticated reindeer (*R. t. tarandus*)

Jouko Kumpula & Alfred Colpaert

In this work we investigated the effects of local weather and snow conditions on the reproduction and survival of semi-domesticated reindeer (*Rangifer t. tarandus*) from 1962 to 1987 in four separate study areas in northern Finland. Reindeer density had no negative effect on calf percentage in slaughter (October–January) in any area. The higher the number of very warm days or mean temperatures in summer, the lower was the calf percentage in all forested areas (Sodankylä, Muonio and Ivalo). In the Muonio area, calf percentage was also reduced by winters with abundant snow accumulation. In the open, mountainous Kevo area, calf percentage was reduced with a high number of warm days (mean T > 0 °C) during the previous December. However, if the previous May was warm in that area, it had an opposite effect. High reindeer densities seemed to increase mortality only in the Sodankylä area. Abundant snow accumulation during winter reduced the survival index of reindeer both in the Sodankylä and Ivalo areas. In the Muonio area, mortality of reindeer was increased with a high number of warm days in December. In the Kevo area, reindeer density or any climatic parameters could not explain yearly differences in mortality. This study indicated that permanent changes in climatic conditions could have different impacts in woodland as opposed to open, mountainous regions. In general, if global climatic change means weather instability in early winter and more snow, it also brings more difficulties for reindeer. However, if climate change means that snow melts earlier in the spring, some conditions could become more favourable for reindeer.

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It is a commonly accepted tenet that the population dynamics of ungulates in predator-free environments are strongly influenced by a combination of stochastic variation and population density (Messier 1991; Sæther 1997; Portier et al. 1998; Milner et al. 1999; Aanes et al. 2000). As a consequence of stochastic variation, a fixed, stable equilibrium between herbivores and their food plants is unlikely to exist in natural grazing systems (Ellis et al. 1991; Behnke & Scoones 1992; Aanes et al. 2000). However, it has also been observed that population size can oscillate within certain limits in many herbivore populations. Therefore it can be supposed that within a longer period population density can fluctuate around some mean density with a certain variance (Murdock 1994; Turchin 1995; Sæther 1997).

It can be also supposed that in reindeer (*Rangifer t. tarandus*) and caribou (*R. t. groenlandicus*) populations the main source of stochastic variation is of climate-mediated origin. Thus, knowledge of the effects of various weather and snow

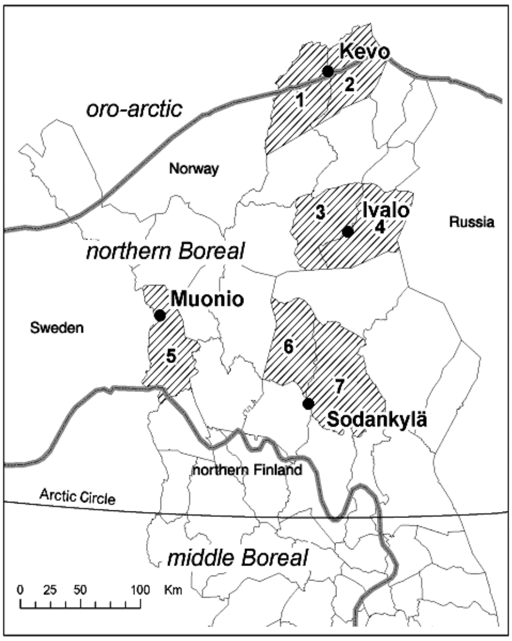

Fig. 1. The Finnish reindeer management area and the four separate study areas. Location of the stations of the Meteorological Institute in the study areas have been marked. Reindeer management districts in Kevo are (1) Paistunturi and (2) Kaldoaivi; in Ivalo (3) Hammastunturi and (4) Ivalo; in Muonio (5) Muonio and in Sodankylä (6) Sattasniemi and (7) Oraniemi.

conditions on the demography of reindeer and caribou populations helps us to understand better the fluctuations of productivity and animal density in these populations. However, if or when stochastic variation is bounded into certain limits, animal density and pasture condition are important measures when trying to optimize pasture use and productivity of reindeer or caribou herds in a long run (Klein 1968; Skogland 1985, 1986; Ouellet et al. 1997; Kumpula et al. 1998; Fynn & O'Connor 2000; Kumpula, Colpaert et al. 2000; Kumpula 2001a; Moxnes et al. 2001).

There is also an interaction between population density and climatic variables, i.e. the effect of climate is stronger at high than at low reindeer densities (Aanes et al. 2000). This is probably because at high animal densities pastures tend to deteriorate and the intensity of direct food competition increases (Klein 1968; Leader-Williams et al. 1987; Henry & Gunn 1991; Manseau et al. 1996; Augustine et al. 1998; Crête & Doucet 1998; Alpe et al. 1999; Kumpula, Colpaert et al. 2000). Especially difficult snow conditions in winter can increase mortality and reduce the reproduction rate in genus *Rangifer* (Klein 1968; Helle 1980; Reimers 1982; Adamczewski et al. 1988; Kumpula & Nieminen 1992; Adams & Dale 1998; Aanes et al. 2000). Another factor explaining much of the yearly variation in body weights of reindeer and caribou in autumn, and also affecting calf mortality, is the level of insect harassment, which has been found to correlate with daily temperatures and wind speed in summer (Helle & Tarvainen 1984; Mörschel & Klein 1997; Mörschel 1999). A large number of parasitic insects affects reindeer and caribou mainly by decreasing grazing and increasing energy expenditures.

The objective of this work was to study the effects of local weather and snow conditions on the reproduction and survival of semi-domesticated reindeer (*R. t. tarandus*) in four areas in northern Finland. Vegetation, pastures, topography and climatic conditions differ among the study areas. One important aspect was therefore to look at which weather effects were the most detrimental in each area. Reproduction and survival of reindeer were studied before 1987 because since then supplementary feeding of reindeer has improved the condition of reindeer, masking the effects of adverse weather conditions (see Kojola et al. 1995; Kumpula et al. 2002).

Material and methods

Weather and snow data from 1961 to 1987 were obtained from four stations of the Finnish Meteorological Institute (Sodankylä, Muonio, Ivalo and Kevo) in nothernmost Finland (Fig. 1). The following parameters for each month were used: mean temperature, maximum temperature, minimum temperature, total precipitation (mm), snow depth on the 15th day, number of days when the mean temperature exceeded 0 °C, 5 °C and 15 °C, and number of days when the maximum temperature was higher than 25 °C. Also calculated were mean temperature and total precipitation for January–February, March–April, June–August, September–October and November–December. For the whole summer period (June–August), the following parameters were calculated: the number of days when the mean temperature exceeded 15 °C and the number of days when the maximum temperature was higher than 25 °C. The sum of monthly snow depths was calculated for November–December, January–February, March–April and then November–April. The difference in mean temperature between December and November was also calculated.

Calf percentage (calves per 100 females) in round-ups (October–January) and the mortality index of reindeer and reindeer density (reindeer/km² land area, winter stock) were calculated for each year from the statistics of the Finnish Reindeer Herders' Association in the four study areas (Fig. 2). The survival index of reindeer was calculated comparing the number of adult (over 1 year old) reindeer counted in round-ups to the number of all reindeer left alive (adults + calves) in the previous year. The survival index was therefore the combination of natural mortality and counting accuracy of reindeer so that both of these elements affected the size of counted reindeer population in a certain year compared to the previous year. Although counting accuracy of reindeer has varied between years, the survival index still reflects a certain level of mortality relatively well in statistical analyses. Calf percentage and the yearly survival index were the means of two reindeer management districts in three of the study areas. These reindeer management districts were in the Sodankylä area Oraniemi and Sattasniemi, in the Ivalo area Ivalo and Hammastunturi, and in the Kevo area Paistunturi and Kaldoaivi. In the Muonio study area only the Muonio reindeer management district was included in the analysis (Fig 1). Alternations of mean calf percentage, mortality index and reindeer density in the period 1962–1987 are given in Fig 2.

On the basis of the data from the Finnish Metorological Institute, the mean temperature of the coldest month—February—during 1961–1990 has been –13.6 °C in Sodankylä, –14.5 °C in Muonio, –13.0 °C in Ivalo and –14.1 °C in Kevo. The mean temperature of the warmest month—July—in the same period has been +14.1 °C in Sodankylä, +13.7 °C in Muonio, +13.7 °C in Ivalo and +12.7 °C in Kevo. Mean snow depth in March during 1961–1990 has been 72 cm in Sodankylä, 68 cm in Muonio, 65 cm in Ivalo and 66 cm in Kevo.

The Sodankylä, Ivalo and Muonio study areas lie within the northern Boreal zone. Both in the Muonio and Ivalo study areas, dry and very dry pine forests as winter pastures are much more common than in the Sodankylä area, where submesic and mesic spruce forests have replaced these pastures in late winter. The Kevo area belongs to the Fjell Lapland birch forest zone where dry and very dry mountain birch forests (*Betula pubescens* var *tortuosa*) and heaths above the tree line form the main winter pastures. During the study period reindeer grazing on natural pastures in the Sodankylä area obtained their food in early and mid-winter mainly by digging reindeer lichens (*Cladonia* spp.) and other terrestial plants (like grass, sedges and dwarf shrubs), but in late winter they browsed mainly arboreal lichens (*Alectoria*, *Bryoria* spp.) in spruce forests. In the other three study areas, reindeer lichens and other terrestial plants dominated the diet of reindeer during the whole winter (Helle & Saastamoinen 1979; Kojola et al. 1995).

Very large open mires are typical of the Sodankylä area and form the most important summer pasture type there. Although there are considerably fewer mires in the Muonio area than in the Sodankylä area, mires still have some importance as summer pastures in Muonio. In contrast, in the Ivalo area there are very few mires areas and submesic forests replace mires as summer pastures. In the Kevo area reindeer use mainly submesic birch forests and some mires as summer pastures. The terrain in the Muonio area and even more so in the Ivalo and Kevo areas is much more rugged and hilly than in the Sodankylä area, which is relatively flat.

Dependency of calf percent and the yearly survival index on weather and snow parameters in the previous year were first analysed with simple regression models. Then reindeer density and only those parameters correlating significantly ($P \leq 0.05$) with the calf percentage and survival index were used in GLM analyses. After that, GLM analyses with backwards stepwise (with alpha-to-remove = 0.05) were made with the same independent variables in order to find the most predictive parameters for reproduction and mortality.

Results

Contrary to what could be expected, high reindeer densities did not seem to correlate negatively with a low calf percentage in any area (Table 1). In the Sodankylä and Ivalo areas, calf percentage was high when reindeer density was high. When looking only at the effects of weather and snow conditions on calf percentage in the stepwise GLM analyses, the higher the number of very warm days or mean temperatures in summer, the lower

Table 1. Effect of reindeer density and weather on calf percentage (calves/100 females) in the study areas, 1962–1987: results of ordinary GLM analyses and GLM analyses with stepwise command. RDEN stands for reindeer density (reindeer/km²) during the previous winter. MTJULY is the mean temperature (°C) in July. DAY0DEC is the number of days in December when the mean temperature is above 0 °C. DIFTDECNOV is the difference in mean temperatures between December and November. MAX25JUL is the number of days in July when the maximum temperature is above 25 °C. SNACWIN is the sum of the monthly snow depths (on the 15th day of the month) from November to April (cm). MTJUNE is the mean temperature (°C) in June. MTAUG is the mean temperature (°C) in August. MAX25JUNAUG is the number of days from July to August when the maximum temperature is above 25 °C. DAY0MAY is the number of days in May when the mean temperature is above 5 °C.

Study area		Effect	Coefficient	SE	Std. coef.	Tolerance	T	P
Sodankylä	Ordinary GLM:	Constant	45.367	20.623	0.000	–	2.200	0.040
		RDEN	24.015	5.007	0.659	0.926	4.797	0.000
		MTJULY	–2.258	1.393	–0.250	0.732	–1.620	0.121
		DAY0DEC	–0.061	1.352	–0.008	0.590	–0.045	0.964
		DIFTDECNOV	–0.531	0.430	–0.220	0.554	–1.236	0.231
		$R^2=0.650$, $n=25$, $F=9.294$, $P=0.000$						
	Stepwise in:	Constant	60.929	17.604	0.000	–	3.461	0.002
		RDEN	25.272	4.829	0.694	1.000	5.233	0.000
		MTJULY	–3.262	1.195	–0.362	1.000	–2.731	0.012
		$R^2=0.613$, $n=25$, $F=17.458$, $P=0.000$						
Muonio	Ordinary GLM:	Constant	56.692	21.406	0.000	–	2.555	0.020
		RDEN	6.626	3.813	0.326	0.759	1.738	0.099
		MAX25JUL	–1.321	1.121	–0.264	0.532	–1.178	0.254
		DAY0DEC	–1.157	3.287	–0.088	0.432	–0.352	0.729
		DIFTDECNOV	–0.093	0.514	–0.040	0.550	–0.180	0.859
		SNACWIN	–0.062	0.055	–0.281	0.432	–1.129	0.274
		$R^2=0.518$, $n=24$, $F=3.876$, $P=0.015$						
	Stepwise in:	Constant	78.725	11.163	0.000	–	7.052	0.000
		MAX25JUL	–2.031	0.840	–0.406	0.951	–2.418	0.025
		SNACWIN	–0.096	0.037	–0.439	0.951	–2.418	0.016
		$R^2=0.436$, $n=24$, $F=8.126$, $P=0.002$						
Ivalo	Ordinary GLM:	Constant	79.392	28.931	0.000	–	2.744	0.013
		RDEN	13.056	2.976	0.585	0.709	4.387	0.000
		MTJUNE	–0.200	1.275	–0.027	0.439	–0.157	0.877
		MTAUG	–2.465	1.865	–0.187	0.632	–1.321	0.203
		MAX25JUNAUG	–0.897	0.550	–0.287	0.406	–1.631	0.120
		PRECMAY	0.129	0.143	0.124	0.672	0.903	0.378
		SNACWIN	–0.069	0.032	–0.265	0.828	–2.148	0.046
		$R^2=0.773$, $n=25$, $F=10.212$, $P=0.000$						
	Stepwise in:	Constant	32.262	4.246	0.000	–	7.598	0.000
		RDEN	15.502	2.689	0.695	0.982	5.766	0.000
		MAX25JUNAUG	–1.147	0.376	–0.367	0.982	-3.049	0.006
		$R^2=0.686$, $n=25$, $F=24.050$, $P=0.000$						
Kevo	Ordinary GLM:	Constant	1.126	15.543	0.000	–	0.072	0.943
		RDEN	5.278	3.354	0.294	0.810	1.574	0.131
		DAY0DEC	–3.037	1.691	–0.316	0.916	–1.796	0.088
		DAY0MAY	1.322	0.639	0.377	0.854	2.070	0.052
		$R^2=0.433$, $n=24$, $F=5.083$, $P=0.009$						
	Stepwise in:	Constant	6.004	15.758	0.000	–	0.381	0.707
		DAY0DEC	–3.783	1.679	–0.394	0.995	–2.253	0.035
		DAY0MAY	1.700	0.612	0.485	0.995	2.777	0.011
		$R^2=0.362$, $n=24$, $F=5.966$, $P=0.009$						

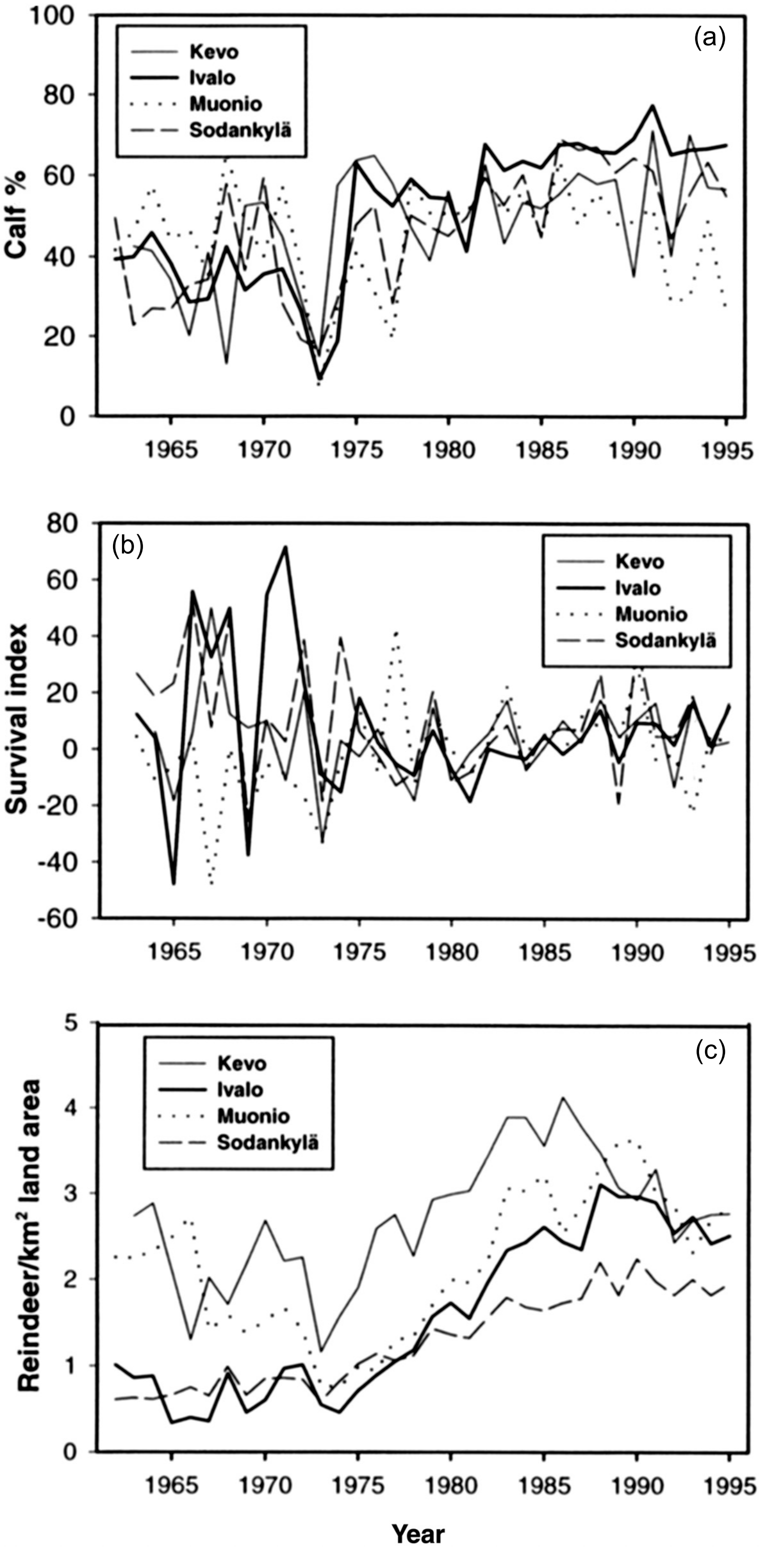

Fig. 2. (a) Variation in mean yearly calf percentage (calves/100 females) in round-ups (October–January); (b) the survival index of reindeer; and (c) reindeer density (reindeer/km² land area, winter stock) between 1962–1987 in the study areas. Original data were obtained from the statistics of the Finnish Reindeer Herders' Association.

was the calf percentage in the next year round-ups in all forested areas in Sodankylä, Muonio and Ivalo (Table 1). This did not seem to apply in the cooler and more mountainous Kevo area. In the Muonio area, the calf percentage was also reduced by winters with abundant snow accumulation. In the Kevo area, the greater the number of warm days (mean $T > 0\,°C$) in December and the lower their number in May, the lower was the calf percentage in the next autumn round-ups.

Of all weather variables, abundant snow accumulation during winter was the only one which seemed to reduce the survival index of reindeer in both the Sodankylä and Ivalo areas (Table 2). In the Sodankylä area, where reindeer used mainly arboreal lichens in late winter, abundant snow accumulation in March and April seemed to be the most important factor for high mortality. In the Ivalo area, where reindeer got their food by digging (cratering) throughout the winter, abundant snow accumulation during the whole winter period increased mortality. Also, high reindeer densities seemed to increase mortality in the Sodankylä area. In the Muonio area, mortality of reindeer was increased when the number of warm days in December was high. In the Kevo area, neither reindeer density nor any weather or snow parameters could explain yearly differences in the survival index.

Discussion

On the basis of this work and previous studies (e.g. Kumpula & Nieminen 1992; Helle & Kojola 1993), a marked increase in reindeer density in Finland since the mid-1970s did not seem to have any negative effect on the reproduction of reindeer. This is probably associated with changes in management practice, including supplemental feeding in the southern half of the area (Helle & Kojola 1993), and calf harvest (Kojola & Helle 1993; Kumpula et al. 1998), which made the herds strongly female-biased and thus improved the survival rate of the stock. It may also be related to the favourable climatic conditions prevailing during the 1980s (Helle et al. 2001). It is very probable that when there is a period of favourable weather and snow conditions, as in our 1980s study period, reproduction is not directly affected by reindeer density. It has been also demonstrated in Norway that the reproduction of adult female reindeer was not controlled by population density, although sub-adult fertility was reduced at high animal densities (Skogland 1985).

In our study, survival of reindeer was reduced at high reindeer densities only in the Sodankylä area, where winter pastures were located both in pine and spruce forests. This density dependence may be linked to the fact that the amount of lichen pasture per reindeer in the Sodankylä area has been the smallest of the four study areas, which may have caused more competition between reindeer in pastures at high densities. Due to the lack of lichen pastures, reindeer in the Sodankylä area have also had to graze mainly arboreal lichen in late winter. It may also be supposed that reduction of survival has probably been caused by increased juvenile mortality in winter since juvenile survival has been observed to be the most sensitive to changes in reindeer density (Skogland 1985).

Some clear dependence between local climatic and productivity factors of the semi-domesticated reindeer stock was found. In all forested areas, summer temperatures had a clear effect on calf production. High mean temperatures and large number of very warm days during summer months seemed to reduce calf production. Warm weather activates blood-sucking insects and keeps reindeer continuously moving in dense herds and may reduce their grazing and resting times (Helle & Tarvainen 1984; Helle & Kojola 1994; Mörschel & Klein 1997; Mörschel 1999). This may exhaust especially smaller calves if calf marking also occurs during a very warm period. Especially in woodland area where where high, open, windy ridges and hilltops are not available, blood-sucking insects and high temperatures in summer can form a very exhausting combination for calves.

Snow accumulation in the previous winter seemed to be an important factor for determining calf percentage or mortality in all three forested areas. The importance of snow depth in the previous winter for ungulate reproduction and body weight has been identified earlier (Helle & Kojola 1994; Adams & Dale 1998; Loison et al. 1999); deeper snow means usually more digging for food and thus more energy costs (Kumpula 2001b). However, it seems that in the Kevo area—where there are a lot of open, windy ridges and hilltops with shallow snow—snow accumulation itself has not had any direct effects on calf production or mortality. The Kevo Meteorological Station is located in a deep valley, which can mean that snow conditions in the adjacent mountain area are inaccurately registered. However, snow accumulation can affect calf production even in mountain areas: one recent study (Helle et al. 2001) has shown that snowy winters reduced the calf percentage and affected yearly change in population size in the Käsivarsi mountain area, which is located nearer the western coast of northern Scandinavia than our study area.

Generally, there seems to be three important periods for succesful reproduction and survival in a year: early winter, spring and mid-summer. Weather and snow conditions, particularly in December, essentially affect the development of those conditions which regulate the availability and quality of terrestrial winter food (Kumpula, Parikka et al. 2000). If there are warm Decembers with temperatures fluctuating around 0 °C, a hard snow or ice layer can form on vegetation which then hampers foraging during the whole winter. This is probably a more important factor than snow accumulation itself in open, high pasture areas compared to woodland pasture areas. Especially in woodland areas, a thick snow layer on unfrozen soil in early winter can hamper digging but may also promote the growth of certain micro-fungi on vegetation (Kumpula, Parikka et al. 2000). These micro-fungi may then be harmful for the reindeer health. The body condition of reindeer females during calving is thus much affected by weather and snow conditions in late autumn and early winter. For reindeer herders, early winter vegetation and snow conditions, which may then affect the availability and quality of terrestrial food during the rest of the winter,

Table 2. Effect of reindeer density and weather on the survival index of reindeer in the study areas, 1962–1987: results of ordinary GLM analyses and GLM analyses with stepwise command. RDEN stands for reindeer density (reindeer/km²) during the previous winter. SNACMAYAPR is the sum of the monthly snow depths (on 15th day of the month) from March to April (cm). DAY0DEC is the number of days in December when the mean temperature is above 0 °C. SNACWIN is the sum of the monthly snow depths (on the 15th day of the month) from November to April (cm).

Study area		Effect	Coefficient	SE	Std. coef.	Tolerance	T	P
Sodankylä	Ordinary GLM:	Constant	110.962	20.150	0.000	.	5.507	0.000
		RDEN	–16.681	7.584	–0.322	0.986	–2.199	0.039
		SNACMAYAPR	–0.587	0.121	–0.712	0.986	–4.859	0.000
		$R^2=0.556$, $n=24$, $F=13.127$, $P=0.000$						
	Step-wise in:	the same as above						
Muonio	Ordinary GLM:	Constant	0.471	20.604	0.000	.	0.023	0.982
		RDEN	1.449	4.128	0.060	0.839	0.351	0.729
		DAY0DEC	–11.331	3.534	–0.692	0.522	–3.206	0.004
		SNACWIN	–0.003	0.059	–0.010	0.470	–0.046	0.964
		$R^2=0.514$, $n=24$, $F=7.053$, $P=0.002$						
	Stepwise in:	Constant	2.537	2.865	0.000	–	0.885	0.386
		DAY0DEC	–11.702	2.443	–0.714	1.000	–4.789	0.000
		$R^2=0.510$, $n=24$, $F=22.935$, $P=0.000$						
Ivalo	Ordinary GLM:	Constant	88.799	26.188	0.000	–	3.391	0.003
		RDEN	–7.436	7.127	-0.188	0.996	–1.043	0.309
		SNACWIN	–0.262	0.086	-0.549	0.996	–3.056	0.006
		$R^2=0.324$, $n=24$, $F=5.032$, $P=0.016$						
	Stepwise in:	Constant	78.484	24.299	0.000	–	3.230	0.004
		SNACWIN	–0.257	0.086	–0.538	1.000	–2.990	0.007
		$R^2=0.289$, $n=24$, $F=8.940$, $P=0.007$						

have always been very important to estimate. In our data, the number of warm days in December as well as the difference in average temperatures between December and November probably indicate something about the development of snow conditions as well as soil temperatures and the formation of permanent ground frost in soil in early winter.

May is another important month for successful calf production especially in the northernmost part of the Finnish reindeer management area. After a warm, rainy May, the calf percentage seems to be high. This kind of weather probably causes rapid snow melt and the early emergence of green vegetation (Kumpula & Nieminen 1992) or can simply improve the availability of winter food when snow melts earlier (Helle et al 2001). This will improve the body condition of reindeer females and thus favour calving.

This study indicates that permanent climate changes could affect woodland and open, mountainous areas in different ways. There should be broader knowledge of the effects of local weather conditions, and their variations, on vegetation and reindeer populations and in which way the potential global climatic variation or change affects local weather and snow conditions. One index of global climate fluctuations, the North Atlantic Oscillation (NAO), has been observed to correlate with plant phenology (Post & Stenseth 1998) and snow conditions (Mysterud et al. 2000) in Norway. Plants bloomed earlier following positive NAO (warm, wet) winters, but the timing of flowering varied with the NAO more strongly in southern than in northern Norway. Early-blooming plants were more strongly influenced by the NAO than late-blooming plants. Snow depth was negatively correlated with the NAO at low altitudes but this relationship was reversed at high altitudes, giving a positive correlation between snow depth and the NAO.

It has been also shown that positive NAO winters with high precipitation and warm weather are mostly adverse for ungulate populations in northern latitudes (excluding the coast of Norway and the Isle of Rum, Scotland), reducing body weight, reproduction and population growth rate and increasing mortality (Post & Stenseth 1999; Mysterud et al. 2000). The NAO index has also been observed to have a strong impact on the population dynamics of semi-domesticated reindeer in the Käsivarsi area, northern Finland (Helle et al. 2001). Reduction of calf production and population size followed both highly negative and positive NAO winters.

This work has shown that variation in local weather and snow conditions, especially in early winter and spring, as well as snow accumulation during winter, could have a strong impact on the reindeer population in northern Finland. The clear impacts of summer temperatures on calf production of reindeer were also demonstrated. It is evident that if global climatic change means higher instability of weather in early winter and more snow during the whole winter in northern latitudes, conditions become more difficult for reindeer. These effects can be even more adverse if summer temperatures rise high. On the other hand, if climate change brings earlier snow melting in spring, it can make some conditions more favourable for reindeer.

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