Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability

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Abstract: To understand the factors influencing life history traits and population dynamics, attention is increasingly being given to the importance of environmental stochasticity. In this paper, we review and discuss aspects of current knowledge concerning the effect of climatic variation (local and global) on population parameters of northern ungulates, with special emphasis on reindeer/caribou (*Rangifer tarandus*). We also restrict ourselves to indirect effects of climate through both forage availability and quality, and insect activity. Various authors have used different weather variables; with sometime opposite trends in resulting life history traits of ungulates, and few studies show consistent effects to the same climatic variables. There is thus little consensus about which weather variables play the most significant role influencing ungulate population parameters. This may be because the effects of weather on ungulate population dynamics and life history traits are scale dependent and it is difficult to isolate climatic effects from density dependent factors. This confirms the complexity of the relationship between environment and ecosystem. We point out limits of comparability between systems and the difficulty of generalizing about the effect of climate change broadly across northern systems, across species and even within species. Furthermore, insect harassment appears to be a key climate-related factor for the ecology of reindeer/caribou that has been overlooked in the literature of climatic effects on large herbivores. In light of this, there is a need for further studies of long time series in assessing effects of climate variability on reindeer/caribou.

Key words: body mass, caribou, climate change, fecundity, insect harassment, moose, NAO, North Atlantic Oscillation, red deer, reindeer, sex ratio, survival, weather.

Introduction

Determining the causes of spatio-temporal variation in life history traits among individuals is one of the main goals of ecology (Begon *et al.,* 1996). This requires long-term studies, accurate estimates of population sizes and demographic parameters, as well as identification of the important factors influencing the traits (Loison *et al.,* 1999a). Most of the life history traits are influenced by a great number of intrinsic and extrinsic interactions that determine the developmental process of populations (Cappuccino & Price, 1995). In efforts to under-

stand the importance of factors influencing life history traits and population dynamics of northern ungulates, attention is increasingly being given to the importance of environmental stochasticity (Murdoch, 1994; Turchin, 1995; Putman *et al.,* 1996; Sæther, 1997). Density-independent variation in phenotypic traits can, if persistent, contribute substantially to population fluctuations in ungulates (Sæther, 1997). Some general patterns have emerged showing, for example, that recruitment is affected more than adult survival (Grubb, 1974; Sæther, 1997; Gaillard *et al.,* 1998). However the effects of weather on population dynamics in herbivores still remain only superficially understood (Sæther, 1997).

Climate may act directly on animal behaviour at different scales (Helle, 1984; Skogland, 1989; Kojola, 1991). For example, the direct effect of severe cold or chilling due to rainfall may lead to increased costs of thermoregulation (Parker & Robbins, 1985; Putman *et al.,* 1996), and increasing snow depth to increased costs of locomotion in snow (Parker *et al.,* 1984). Climate also acts indirectly on ungulate population parameters through its effect on plants. Indeed, climatic conditions are known to have major impact on abundance and nutritional quality of plant tissues available to herbivores (Deinum, 1984; Van Soest, 1994). For some northern ungulates, much of the variation in population parameters has been related to the availability of resources in either winter (Skogland, 1985) or summer (Reimers *et al.,* 1983; Reimers, 1997; Hjeljord & Histøl, 1999; Finstad *et al.,* 2000a).

There have been recent reviews on the effects of climate on large herbivores (Sæther, 1997) and the effects of climate in specific geographic areas with either fairly mild (U.K.; Putman *et al.,* 1996) or extreme climates (Gunn & Skogland, 1997; Klein, 1999). However, there has not been a synthesis of the recent new advances in assessing climatic effects on northern ungulates with an emphasis on mechanisms, and reindeer in particular. Sæther (1997) stressed the need for a better understanding of the mechanistic basis behind climatic effects on large herbivores. In this paper, we review and discuss central aspects of the current knowledge concerning the effect of climate (local and global) on population dynamics and life history traits of northern ungulates, with emphasis on reindeer and caribou (both *Rangifer tarandus*). We also consider recent advances regarding possible mechanisms, but restrict our focus to indirect effects of climate mainly on plant quantity and quality, and their nutritional importance in the population dynamics of northern ungulates as suggested by Post &

Stenseth (1999). Furthermore, we discuss the indirect effect of climate through insect harassment on reindeer/caribou, an aspect that has been largely overlooked by reviews in this field. Indeed, climate also acts indirectly on some ungulates, as in the case of reindeer and caribou, through interaction with insects that affect their population parameters (Anderson *et al.,* 1994; Gunn & Skogland, 1997; Mörschel & Klein, 1997; Mörschel, 1999; Colman, 2000). A more thorough understanding of these mechanisms is made more urgent by global climate changes that are affecting most northern areas (Hughes, 2000).

Climatic variability and plant responses

Plant adaptation

Because of stochastic variation in climate, plants may develop different survival strategies to cope with unfavourable environmental conditions. Taiz & Zeiger (1999) called this «stress tolerance». At northern latitudes, unfavourable and harsh environmental conditions can be persistent (Heide, 1985), and plant responses to these conditions include acclimation, as well as adaptation. Because of the short growing season and generally low temperature and variation in photoperiod in the north, light and temperature are suggested to be the most important factors influencing plant growth and development (Van Soest, 1994). Because moisture stress is an important factor during winter for trees, leaf shedding and winter bud formation are important adaptations (Levitt, 1980). Early leaf development enables perennial and herbaceous plants to utilize short and cool growing seasons, and plants adapt to water stress by a limitation in leaf expansion (Taiz & Zeiger, 1999)

Local climatic variation and forage quality and quantity

Although nutrients, water, light and heat are necessary for growth of plants, they have to participate in appropriate proportions for optimal plant growth (Jurïsson & Raave, 1984). Yearly variation in forage quality is strongly influenced by weather (Bø & Hjeljord, 1991; Finstad *et al.,* 2000b). Because of the difference in radiation received at the soil surface, Bennett & Mathias (1984) found a more than two fold difference in above ground growth in some plant species as a consequence of slope exposure and associated differences in radiation received at the soil surface. Snow cover and depth affect length of the growing season and hence forage quality (Hjeljord & Histøl, 1999; Van der Wal *et al.,* 2000). Timing of snowmelt also

influences timing of emergence of forage plants (Klein, 1985; Langvatn *et al.,* 1996; Post & Klein, 1999). Most importantly, in years of deep snow there is a prolonged period of access to newly emergent forage due to a variable time of snow melt. Finstad *et al.* (2000a) found that annual variations in summer weather influenced forage availability and digestibility through, for example the variation in the Growing Degree Days in May and June. Sand *et al.* (1996) reported that high crude protein levels in birch (*Betula* sp.) were associated with years having low temperatures and high amounts of precipitation in early summer, and high temperatures in late summer. High environmental temperatures, however, often lead to increased lignification of plant cell walls, lowering digestibility. Amino acids and protein require sugar for their synthesis, therefore an increased nitrogen supply can reduce the sugar content of plant tissues, and this effect is promoted at high temperatures and high light intensity (Deinum, 1984). Cloud cover and shade have been thought to decrease production of the aboveground plant biomass and the nutritive value of forage by affecting the amount of light received by plants (Van Soest, 1994). This may be valid where plants require high light intensity and temperature for optimal growth under short day length at lower latitudes. Restricted light due to cloud cover and, in the case of forest floor vegetation, to shade from the crowns of trees, however, may improve quality of leaf tissue as forage by extending early stages of phenology. This results in a low ratio of structural to photosynthesising tissues and limits accumulation of digestion-inhibiting secondary chemicals derived from carbon that may otherwise be produced in excess of growth needs of plants (Bryant *et al.,* 1983). Bø & Hjeljord (1991) found that continental moose ranges improve during cloudy, wet summers. They reported, after investigation on the most important browse species (*Betula* sp.), that with a decrease in solar radiation, there is an increase in the crude protein:dry matter ratio and a decrease in the tannin content of forage plants. At high latitudes in summer, the short and cool nights have a positive effect on forage quality because there is little respiratory loss by plants at night (Klein, 1970a) and slow build up of fibrous tissues. As winter weather varies annually, snow condition might also vary. Therefore, the availability of forage to ungulates during winter will be affected. Indeed, cold weather following wet snow or rain, may lead to ice layers in the snow or «icing» on the ground surface limiting access of herbivores to vegetation. This will affect species feeding mainly in the field layers such as reindeer more in contrast to browser, which could be more flexible.

Global climatic change and plant quality and quantity

Models of climate change predict that global temperature and precipitation will increase within the next century, the changes being more pronounced in northern latitudes and during winter (Dickinson, 1986; Maxwell, 1997). Warming trends and increased precipitation have been recorded in many regions of the Arctic during the past century, consistent with these climate models (Chapman & Walsh, 1993; Serreze *et al.,* 1995). Brotton & Wall (1997) also mentioned increased winter snowfall in the Northwest Territories of Canada. Both these past and projected climate changes may have affected or may affect the quality and quantity of plant material available as forage for ungulates through changes they bring about in heat, moisture and available soil nutrients during the plant growth season (Klein, 1999). In areas of the high Arctic that may experience warmer and longer plant growth periods with sufficient available moisture, there will be an increase in plant biomass (Klein, 1999). Post & Stenseth (1999) found that the North Atlantic Oscillation (a measure of large-scale climatic variability; see below) was significantly related to plant phenology, as most plant species bloomed earlier following increasingly warm, wet winters with herbaceous species being more sensitive to climatic variation. This could have an effect on length of the growing season which, when extended, has the converse effect of shortening the winter period of plant dormancy (Klein, 1999). This would further lead to increase in winter forage, but with variable quality (Chapin & Shaver, 1996). The projected increase in cloud cover during summer could result in an extension of the period when forage is highly digestible and has relatively low levels of secondary chemicals (Ball *et al.,* 1999; Klein, 1999). This could be of great ecological importance at higher latitudes where the plant growth season is short.

Local climate regime and large herbivore populations

Body weight

Body weight is one of the most important life history traits (Calder, 1984). Several aspects of the life history of deer are associated with body weight; those factors that affect body weight may also have an important influence on population dynamics (Klein, 1970b; Sæther, 1985).

Several studies have shown a relationship between body weight and conditions on the summer range (Aarak & Lenvik, 1980; Reimers, 1983; Langvatn et al., 1996; Sæther et al., 1996; Hjeljord & Histøl, 1999). Langvatn et al. (1996) suggest that weight gain of red deer (Cervus elaphus) during the early summer growth spurt should be rapid during cool May-June weather. They associated this with retarded phenological development of forage plants during periods of cooler weather, causing leaf:stem ratios and digestibility of plants parts to decline more slowly, thus enhancing quality of the available diet. Climate variables expressed through local weather conditions, therefore, can be expected to have a major effect on forage quality and quantity in summer, with associated affects on ungulate body size or body weight. Climatic variables, both through their direct effects on forage quality and its quantitative availability, can be expected to play a major role in population dynamics of northern ungulates (Table 1).

Sæther (1985) found that a combination of many climatic variables explained a significant portion of annual variation in mean carcass weight of moose (Alces alces) in autumn. Mean summer temperature and summer precipitation were the most important variables. Sand et al. (1996) reported that years with relatively high body mass of moose in Sweden were generally associated with low temperature and high amounts of precipitation in early summer, and with high temperatures and low precipitation in late summer and early fall. They also found a positive correlation, although significant only for adult females, between previous winter snow and body mass, suggesting a delayed effect of weather variables on body mass.

The effects of winter climate appear also to be important, through, for example, the indirect effect of late snow melt on forage quality or snow condition on forage availability, but direct effects may also be important. In years with high snowfall, caribou calves were lighter at 10 months of age and presumably unable to gain sufficient mass by autumn to breed successfully as yearlings (Adams & Dale, 1998). Negative correlations between body mass and severity of the preceding winter have been reported for wild reindeer (Skogland, 1983). Gerhart et al. (1996) associated winter undernutrition with declines in body fat and protein in adult female caribou. This was not the case on Southampton Island, Canada, where caribou condition (measured as bone, muscle and empty body mass) did not appear to be related to the winter severity index (Ouellet et al., 1997). Hjeljord & Histøl (1999) also reported a decrease in autumn

body mass of calves and yearling moose with increasing snow depth during the preceding winter and spring. Furthermore, condition of calves may be poor following winters with low temperature and high snow depth (Sæther & Gravem, 1988; Cederlund et al., 1991). Additionally, Cederlund et al. (1991) found a negative correlation between body mass loss and snow depth. Snow depth has been reported to be the only local climatic variable that has a significant effect on red deer body mass in Sør-Trøndelag, Norway (Loison & Langvatn, 1998; Loison et al., 1999b). Similar negative influence was found on black-tailed deer Odocoileus hemionus (Parker et al., 1993), and white-tailed deer O. virginianus (Moen & Severinghaus, 1981). This differs, however, from results of studies by Ouellet et al. (1997) on caribou, as they did not find any relationship between winter severity and body condition.

Reproductive performance and sex ratios
Age at maturity and fecundity are strongly related to body weight and condition (Lenvik et al., 1988; Gaillard et al., 1992; Jorgenson et al., 1993; Festa-Bianchet et al., 1994; Langvatn et al., 1996; Sæther et al., 1996; Reimers, 1997). Therefore, climatic variation is expected to affect these life history parameters (Table 1), but this relationship may, however, differ regionally due to different selective regimes (Sæther et al., 1996).

Finstad et al. (2000b) reported that the proportion of reindeer yearlings lactating in June was positively related to Growing Degree Days the previous May and June and negatively related to both Growing Degree Days the previous July and snow depth the winter prior to birth. Cameron et al. (1993), reported that the probability of a successful pregnancy of female caribou may be largely predetermined during the previous breeding season, based on autumn condition, whereas maternal condition during late pregnancy has greatest influence on calving date and early calf survival. Sand et al. (1996) found in Sweden that high fecundity and recruitment rate of moose were associated with years having relatively warm September weather. The proportion of 2-year-old red deer calving in Norway, and cohort differences in the proportion calving as 3-year-old red deer on Rum, Scotland, were negatively related to variation in May-June degree days 12 months earlier (Langvatn et al., 1996). They also revealed that the proportion of hinds calving on Rum had a tendency to decline with increasing number of days with snow in winter. Winter conditions, thus also influence reproduction. The reproductive performance of female

caribou (2, 3, 4 and 6 year olds) was affected by winter snowfall with natality declining with increasing late winter snow fall during the winter prior to the autumn breeding season (Adams & Dale, 1998). In Southern Norway Sæther et al. (1996) found that female moose also matured earlier after two winters with almost no snow cover. Similarly, delayed maturity was found on mountain goats *(Oreamnos americanus)* in a population living under harsh winter conditions (Jorgenson et al., 1993). Kruuk et al. (1999) found that fecundity of female red deer decreased with rainfall in the preceding winter.

Recently, climate variables have been demonstrated to affect population sex ratios in red deer (Kruuk et al., 1999; Post et al., 1999b; Mysterud et al., 2000). The proportion of male red deer born yearly on the island of Rum, Scotland, declined with winter rainfall, associated with increased nutritional stress in females (Kruuk et al., 1999). In Norway, the proportion of male red deer harvested during autumn each year declined with increasing snow depth in March (Mysterud et al., 2000). The annual sex-ratio was not related to e.g. sex-dependent mortality during the summer season. Female red deer thus reared fewer sons as nutritional stress increased with increasing severity of climate both on Rum, Scotland and in Norway. The extrinsic modification of ungulate sex ratios by climate occurs at a population scale and is probably not adaptive (Kruuk et al., 1999; Post et al., 1999b; Mysterud et al., 2000). However, the physiological mechanism by which sex ratio is determined remains unknown (Hewison & Gaillard, 1999). Possible mechanisms include a higher *in utero* mortality of males under harsh conditions, and modification of the sex ratio at conception and/or implantation (Reimers, 1999; Mysterud et al., 2000).

Survival, abundance and population growth
A close relationship has been reported between winter weather and both annual mortality rate in several species of ungulates (Martinka, 1967; Clutton-Brock & Albon, 1982; Sauer & Boyce, 1983; Skogland, 1985; Gaillard et al., 1993;) and abundance of calves (Lee et al., 2000). Direct effects of winter climatic conditions on survival are commonly reported, but there may also be effects of summer weather.

Skogland (1985), comparing different wild reindeer herds, revealed a relationship between calf survival rate and the amount of forage available during late winter. Caribou in northwestern Alaska also experienced highest calf mortality in years when snowmelt was relatively late (Fancy & Whitten,

1991). Annual variation in population growth rate in Svalbard reindeer was strongly negatively related to winter precipitation. High growth rate occurred when winters were dry, and the effect of climate was stronger at high densities (Aanes et al., 2000). Survival rates of red deer calves of both sexes were positively correlated with temperature and negatively with snowfall, while only a slight negative effect of day-degrees on yearling survival rate was detected in males and a slight positive effect of day-degree was detected on adult male survival rates (Loison & Langvatn, 1998). A negative effect of winter harshness was found for red deer on Rum, Scotland (Clutton-Brock & Albon, 1982), with a lower male than female survival rate (Table 1). Juvenile mortality was observed to increase during winter with both high population density and high November-January rainfall (Kruuk et al., 1999). Studies by Jorgenson et al. (1997) in bighorn sheep *(Ovis canadensis),* and Loison & Langvatn (1998) did not detect a relationship between winter severity and adult survival. These observations show that there are differences in mortality by sex and age class within a population in response to weather variables. In wapiti *(Cervus canadensis),* calf survival rate correlated positively with July temperature and negatively with November precipitation while cow survival was positively correlated with January temperature, but negatively correlated with May temperature and total July precipitation (Sauer & Boyce, 1983). It is noteworthy that, the effect of climate interacts with population density. Indeed, the effect of winter weather on survival of wapiti cows and calves seemed stronger at high population density (Sauer & Boyce, 1983).

Mortality is sometimes also attributed to summer conditions. Comparing latitudinal gradient both in summer and winter range condition in different Norwegian moose populations, Sæther et al. (1996) found that mortality was highest in the northernmost study area, where most death occurred during summer and very few calves died during winter. They found no relationship between winter food supply and calf mortality. Stubsjøen et al. (2000) found seasonal variation in survival among calves but very little among adults, in three populations of moose in northern Norway. The highest mortality was found among neonates during summer in two populations. The natural mortality of calves was different among regions during both summer and winter. Stubsjøen et al. (2000) attributed part of the natural mortality to severe climatic conditions in both winter and summer. Early survival in roe deer *(Capreolus capreolus)* fawns tended to increase with increasing rainfall in May

Table 1. Northern ungulate population responses to annual local climatic variability.

Species	Demographic and phenotypic parameters	Climatic variables	Trend	Locality	References
Caribou	Calf body mass	Snow fall	-	Alaska, USA	Adams & Dale, 1998
	Natality at 2,3,4 and 6 years old female	Late snow fall	- *	Alaska, USA	Adams & Dale, 1998
	Body condition	Winter severity index	None	Southampton Island, Canada	Ouellet et al., 1997
	Calf mortality	Time of snow melt	-	Alaska, USA & Canada	Fancy & Whitten, 1991
Reindeer	Live calve recorded	Warm winter prior to rut	- *	Northern Finland	Lee et al., 2000
		Wetter winter prior to rut	- !		
		Warmer autumn prior to birth	+ !		
	Body mass	Severity previous winter	-	Norway	Skogland, 1983
	Reproductive performance	Previous May and June Growing Degree Days (GDD)	+	Seward Peninsula, USA	Finstad et al., 2000b
		Previous July GDD and snow depth prior to birth	-		
	Population growth rate	Winter precipitation	- *	Svalbard, Norway	Aanes et al., 2000
Red deer	Body mass	Snow depth	- *	Sør Trøndelag, Norway	Loison et al., 1999b
	Calf survival rate	Temperature	+ *	Sør Trøndelag, Norway	Loison & Langvatn, 1998
	Calf survival rate	Snow fall	- *		
	Adult male survival rate	May to June day – degrees	+		
	Yearling male survival rate	May to June day – degrees	-		
	Fecundity	Cool May June weather	+	Norway and Rum	Langvatn et al., 1996
	Age at maturity	Number of day with snow	- !	Rum	
	Age at maturity	May and June degree days	- *	Norway	
	Fecundity	Preceding winter rain fall	- *	Rum, Scotland	Kruuk et al., 1999
	Birth sex ratio (Proportion of male)	Rainfall November-January	- *		
	Autumn sex ratio (Proportion of male)	Snow depth in March	-	Norway	Mysterud et al., 2000
	Juvenile winter mortality	High November-January rainfall	-	Rum, Scotland	Kruuk et al., 1999
	Male survival rate	Winter harshness	- *	Rum	Clutton-Brock & Albon, 1982

Species	Trait	Climate variable			Location	Reference
Wapiti	Calf survival rate	July temperature	+	!	Wyoming	Sauer & Boyce, 1983
	Calf survival rate	November precipitation	-	*		
	Cow survival	January temperature	+	!		
	Cow survival	May temperature	-	!		
	Cow survival	Total July precipitation	-	*		
Moose	Yearling and adult mass	May-June rainfall	+	!	Grimsö, Sweden	Sand et al., 1996
	Body mass	May-June temperature	-			
	Body mass	Warm September weather	+			
	Adult female mass	First previous winter	+	*		
	Fecundity and recruitment rate	Warm September	+			
	Calf body mass	Winter severity	-	*	Grimsö, Sweden	Cederlund et al., 1991
	Body mass loss	Snow depth	-	*		
	Yearling body weight	Snow depth	-	*	Norway	Sæther, 1985
	Calf and yearling mass	Snow depth	-	*	Southern Norway	Hjeljord & Histøl, 1999
Roe deer	Fawn early survival	May June rainfall	+		France	Gaillard et al., 1997
Black-tailed deer	Body mass	Snow depth	-		Alaska, USA	Parker et al., 1993
White-tailed deer	Body mass	Snow depth	-		New York, USA	Moen & Severinghaus, 1981
Chamois	Cohort survival	High precipitation and low temperature preceding spring	+	*	The Alps, France	Loison et al., 1999a
	Survival	Low degree-day spring	-		The Pyrenees, France	
Mountain goat	Age at maturity	Winter harshness	-		Alberta, Canada	Jorgenson et al., 1993

+ Positive correlation.
- Negative correlation.
! P < 0.10.
* P < 0.05.

and June (Gaillard *et al.,* 1997). The cohort survival of the chamois *(Rupicapra rupicapra)* has been reported to increase when precipitation was high and temperatures were low during the preceding spring in the Pyrenees, while no cohort effect was detected in the Alps, but decreased survival occurred following a low degree-day spring (Loison *et al.,* 1999a). In an investigation of the regional effect of climate on reindeer, Lee *et al.* (2000) found that the number of live calves recorded in northern Finland was negatively related to both warmer and wetter winter weather prior to the rut, and positively to warmer autumn weather prior to birth (Table 1). This study did not specify when live calf numbers were recorded and did not include snow characteristics in their models.

Global climatic regime and large herbivore populations

In the North Atlantic region, winter climatic variability is, to a large extent, explained by a large-scale alternation of atmospheric pressure called the North Atlantic Oscillation (NAO) (Rogers, 1984; Hurrell, 1995). The NAO refers to a meridional oscillation in atmospheric mass with centres of action near Iceland and over the subtropical Atlantic from the Azores across the Iberian Peninsula (Hurrell, 1995). Because the signature of the NAO is strongly regional, its state is quantified annually by a simple index based on the mean deviation from the average sea-surface pressure between the Azores and Iceland, from December through March for the winter. Positive values of the NAO-index characterize unusually warm, wet winters in northern Europe (and unusually cold, dry winters in North America), while negative values characterize unusually cold, dry winters in northern Europe (and warm, wet winters in North America) (Hurrell, 1995). Because the NAO accounts for most of the year to year fluctuations in winter precipitation in northern latitudes (Hurrell, 1995, 1996; Hurrell & Van Loon, 1997) as well as variations in wintertime temperatures on the scale predicted by theoretical models of climate change (Hurrell, 1996), the NAO has a clear potential to affect the ecology of plants and animals in the Northern Hemisphere (Post *et al.,* 1999a). However, as the effect of this large-scale climatic index may result in different local weather patterns in different areas (Mysterud *et al.,* 2000), these interactions are inherently complex.

The NAO, through its effects on vegetation and climatic conditions, influences several aspects of life history and ecology of terrestrial large mammalian herbivores, including phenotypic variation, fecundity, sex ratios, demographic trends and population dynamic processes (Post *et al.,* 1997, 1999a,b,c; Forchhammer *et al.,* 1998; Post & Stenseth, 1998, 1999; Loison *et al.,* 1999a; Mysterud *et al.,* 2000). Global climate change will likely increase both the extent and seasonal duration of open water in the arctic seas, and the frequency of oceanic cyclonic storms at high latitudes (Serreze *et al.,* 1995). Icing events can, therefore, be expected to increase, limiting access to forage by caribou (Klein, 1999). Such broad patterns of global change will affect most herbivore population parameters (See Gunn & Skogland, 1997; Table 2).

Body mass, fecundity and sex ratios
There is a correlation between the NAO and red deer cohort-specific mean body weight and skeletal ratios of adults when cohorts were *in utero* (Post *et al.,* 1997). Recently, however, opposite correlations between the NAO and red deer body weight were reported from the same area in Norway; both high body weights of red deer calves (Loison *et al.,* 1999b) and low body weights of adult red deer (Post *et al.,* 1997) followed years with positive NAO. Mysterud *et al.* (2000) found that the contrasting result was because Post *et al.* (1997) did not control for the stronger and negative effect of local density, as both density and the NAO increased during the span of the study. A high NAO index was indicative of higher precipitation. As winter temperatures at the west coast of Norway is commonly around 0 °C, the warmer temperatures, however, at higher NAO (Hurrell 1995; Post *et al.,* 1997) result in a negative correlation between snow depth and the NAO at low elevation, whereas this relationship is reversed above approximately 400 m a.s.l. (Mysterud *et al.,* 2000). Forage in the field layer is thus probably more easily available to red deer in these coastal and lowland areas during winters with a high NAO index (Loison *et al.,* 1999b), and a high NAO index thus probably indicates favourable conditions for red deer. Indeed, body weights of red deer in Norway in general were positively correlated with the NAO when taking population substructure into account and using an index for local density, although this relationship was reversed at very low NAO values (A. Mysterud, N.G. Yoccoz, N.C. Stenseth & R. Langvatn, unpublished results).

On Rum, Scotland, Post & Stenseth, (1999) observed that birth mass and adult mass of red deer increased following positive (warm, wet) NAO winters while fecundity of female red deer correlated negatively with the NAO index of the winter in

which they were *in utero.* They also reported a negative relationship of both reindeer calf mass and female fecundity with NAO in Finland and Norway respectively (Table 2). On the contrary, Loison *et al.* (1999b) found that body mass of red deer was positively correlated to NAO, but lagged one year. Also, while yearling moose in Norway were heavier if born following positive NAO winters, body mass of moose in Sweden, where winter weather was more continental, declined following warm, wet winters (Post & Stenseth, 1999). This suggests that the effect of NAO on population parameters varies regionally. Post *et al.* (1999c) documented recently that the state of the NAO during fetal development of hinds in red deer influenced the mass of their sons, but not daughters.

Winters with a high NAO index also led to increasingly male biased sex ratios of offspring, independent of changes in the mean age of hinds (Post *et al.,* 1999b; Mysterud *et al.,* 2000; Table 2; see also discussion above). There was, however, no residual effect of the NAO once the effect of snow depth (at low elevation) was controlled for male-biased harvest with increasing snow depth (Mysterud *et al.,* 2000).

Abundance and survival
In red deer, Forchhammer *et al.* (1998) observed that, warm, moist winters (high NAO) were associated with decreased abundance (through over-winter mortality the following year), whereas the delayed two-year effect of warm, moist winters had a positive effect on abundance (through increased fecundity of the cohort born following high NAO), with the positive effects being relatively larger. They suggested that the NAO effect was sex-specific, operating primarily through the female segment of populations. It also has been shown that male and female calves responded differently to climatic variability (Post *et al.,* 1999c). Post *et al.* (1999a) reported that in both Sør-Trøndelag (Norway) and Rum (Scotland), total abundance of red deer increased two years after increasingly warm winters (Table 2). Whereas in Norway, this increase was attributed to the enhancement of cohort specific fecundity of 2 year-old hinds, on Rum it was attributable to increases in annual fecundity of 3 year-old hinds. Indeed, adult male abundance was negatively correlated to the previous NAO on Rum (Post & Stenseth, 1999). Both abundance (Post & Stenseth, 1999) and lamb survival (Milner *et al.,* 1999) of Soay sheep *(Ovis aries)* have also been reported to decrease following high NAO. Loison *et al.* (1999a) found that adult chamois born after positive NAO (indicative of high

temperature and low precipitation in winter) exhibited low winter survival in the Pyrenees, while in the Alps, survival decreased following positive NAO. Accordingly, they suggested that common ideas about effect of winter harshness and snow on survival of herbivores are more complicated than assumed previously.

On the western side of the Atlantic, caribou, moose, muskox *(Ovibos moschatus)* and white-tailed deer abundance increased following high NAO (Table 2) in West Greenland, Isle Royale, East Greenland and Minnesota respectively (Post & Stenseth, 1999). The rates of increase of both moose and white-tailed deer in North America were influenced by global climatic fluctuation at 2 and 3 years lags, as well as delayed density-dependence feedback and wolf predation (Post & Stenseth, 1998).

Climate, insect activity and harassment

Studies discussing effects of climatic variability on ungulate populations have generally not related it to the effects of insects. However, this mechanism may potentially be very important. Klein (1991) suggested that harassment by the skin warble *(Hypoderma tarandi,* Oestridae) and nasal bot flies *(Cephenemyia trompe,* Oestridae), introduced to Greenland in the 1950s, and infestation by their larvae may have been a major factor influencing decline in body condition and suppression of the population of West Greenland caribou. Syroechkovskii (1995) estimated that caribou or reindeer could lose up to 2 kg of blood to mosquitoes during one season in the Taimyr Peninsula, Russia. Colman (2000) reported lower body mass in the southernmost population of reindeer in Norway after a summer with severe insect harassment than after a cool summer (Table 3). It has appeared in the same area and during the same period that free ranging sheep weight was higher in the year with warmer summer (unpubl. data), suggesting that the pasture was not of bad quality, and that insect harassment may affect reindeer/caribou body condition independently of range quality. Considerable behavioural evidence supports harassment by insects as the most important causal link between warm summer temperatures and low body condition of reindeer. Indeed, dense aggregations and associated movement of reindeer and caribou during warm summer weather are associated with insect harassment (Anderson & Nilssen, 1996; Noel *et al.,* 1998), which results in increased time spent moving and/or standing, and reduced time spent feeding, with detrimental nutritional conse-

Table 2. Northern ungulate population responses to the North Atlantic Oscillation (NAO) index.

Species	Demographic and phenotypic parameters	Climatic variable	Trend	Locality	Reference
Caribou	Abundance	Previous NAO	+ *	Sissimiut, West Greenland	Post & Stenseth, 1999
Reindeer	Calf body mass	NAO when *in utero*	-	Finland	Post & Stenseth, 1999
	Adult female fecundity	NAO 1 year previous	- *	Norway	Post & Stenseth, 1999
Moose	Yearling mass	NAO when *in utero*	+ *	Norway	Post & Stenseth, 1998
	Yearling mass	NAO 3 years previous	- *	Sweden	Post & Stenseth, 1999
	Calf body mass	NAO 3 years previous	- *	Sweden	Post & Stenseth, 1999
Red deer	Abundance	NAO previous	-	Norway	Forchhammer *et al.*, 1998
		NAO 2 years lags	+	Norway	
	Total abundance	NAO 2 years previous	+ *	Sør Trøndelag, Norway	Post *et al.*, 1999a
		NAO 2 years lags	+ *	Rum, Scotland	
	Adult male abundance	NAO previous	- *	Rum, Scotland	
	Calf birth mass	NAO when *in utero*	+ *	Rum, Scotland	Post & Stenseth, 1999
	Cohort fecundity (3 years olds + milk hinds)		- *	Rum, Scotland	
	Cohort fecundity (2 years olds)		+ *	Norway	
	Adult female mass		+	Rum, Scotland	
	Adult male mass		+	Rum, Scotland	
	Adult female mass		- *	Norway	Post *et al.*, 1997
	Adult male mass		- !		
		NAO 1 year lag	None	Norway	Mysterud *et al.*, 2000
Chamois	Body mass	NAO 1 year lag	+ *	Sør Trøndelag, Norway	Loison *et al.*, 1999b
	Autumn sex ratio	NAO	+ *	Hordaland, Norway	Post *et al.*, 1999b
	(Proportion of male)	NAO	+ *	Norway	Mysterud *et al.*, 2000
		NAO 1 year lag		Norway	Mysterud *et al.*, 2000
	Survival	NAO 1 year lag	- *	The Alps, France	Loison *et al.*, 1999a
	Adult survival	NAO year of birth	- *	The Pyrenees, France	Loison *et al.*, 1999a
Muskox	Abundance	NAO 1 year previous	+ *	East Greenland	Post & Stenseth, 1999
Soay sheep	Abundance	Previous NAO	- *	Village Bay, UK	Post & Stenseth, 1999
	Lamb survival	NAO	- *	St Kilda, Scotland	Milner *et al.*, 1999
	Adult female survival	NAO	- !	St Kilda, Scotland	Milner *et al.*, 1999
White tailed deer	Population rates of increase	NAO 3 years lags	+ *	Minnesota, USA	Post & Stenseth, 1998
	Population rates of increase	NAO 2 years lags	+ *	Isle Royale, USA	Post & Stenseth, 1998

+ Positive correlation.
- Negative correlation.
! $P < 0.10$.
* $P < 0.05$.

quences (Helle *et al.*, 1992; Toupin *et al.*, 1996; Mörschel & Klein, 1997; Colman, 2000). Using activity change per minute as an indicator of harassment, Mörschel & Klein (1997) reported higher rate of activity changes among caribou in central Alaska when insects were present. Temperature and wind speed had a significant effect on the rate of activity changes of caribou (Table 3), reflecting the regulation of insect activity by these abiotic factors. Behavioural responses to avoid insects are commonly observed. Indeed, as reported by Pollard *et al.* (1996), caribou movements, distribution, and behaviour were significantly influenced by harassment from parasitic insects such as mosquitoes and oestrids, during the post-calving period. Espmark & Langvatn (1979) reported that lying down was a strategy to cope with head fly harassment in red deer in Norway. This indicates a possible detrimental effect of insect harassment also on other species of deer.

Three major parasitic insects are of primary concern for reindeer: mosquitoes (especially *Aedes* sp., Culicidae), warbles flies and nasal bot flies (Gunn & Skogland, 1997; Mörschel & Klein, 1997). But, Anderson & Nilssen (1998) reported evidence for potential contribution to the harassment on reindeer by black flies (Simuliidae) and horse and deer flies (Tabanidae) as well. Roby (1978) observed a higher percentage of standing and running and a lower percentage of lying under oestrid fly harassment than under similar levels of mosquito harassment. Mörschel & Klein (1997) found that the presence of oestrid flies had a larger influence on activity budgets of caribou than did mosquitoes by substantially increasing the amount of time spent standing and decreasing the amount of time spent feeding.

It is during summer, which is the peak period in energy and nutrient intake and requirement for northern

Table 3. Insect responses to climatic variability and related consequences on reindeer/caribou.

Climatic variables	Insect harassment	Resulting reindeer/caribou responses	Locality	Reference
Warm summer	Increase	Aggregation and movement	Norway; Alaska, USA	Anderson & Nilssen, 1996; Noel *et al.*, 1998
Warm summer	Increase	Lower body weight	Southern Norway	Colman, 2000
Temperature	Increase*	Lower body weight		
Cloud cover	Decrease*	Lower body weight		
Warm summer	Increase	Increase time spent moving and/or standing and decreasing time spent feeding	Finland; Norway; Canada; Alaska, USA	Helle *et al.*, 1992; Colman, 2000; Toupin *et al.*, 1996; Mörschel & Klein, 1997
Temperature	Increased*	Increase rate of activity change	Alaska, USA	Mörschel & Klein, 1997
Wind speed	Decreased*			
Cloud cover	Decrease			
Relative humidity	Increase			
Wind speed	Decrease	Lower disturbance	Alaska, USA	Walsh *et al.*, 1992
Temperature	Increase mosquito abundance	Higher disturbance	Alaska, USA	Pollard *et al.*, 1996
Wind velocity	Decrease mosquito abundance	Lower disturbance		
Relative humidity	Decrease mosquito abundance	Lower disturbance		

* $P < 0.05$.

ungulates that harassment by insects occurs. Russell (1993) reported that the warble and nasal bot fly season lasted from the end of June until early August, while mosquitoes were primarily a problem in July. In Norway the oestrid season lasts from 10 July and ends around 20 August (Nilssen & Haugerud, 1994). Although there is considerable range in how the combination of weather variables affect levels of insect harassment, it is clear that temperature, wind and relative humidity are the primary interacting factors for reindeer and caribou, the relative importance of each varying with terrain features, location (altitude and latitude), vegetation and substrate type, and animal group size and behaviour. Walsh et al. (1992) used an ambient temperature «greater-than-or-equal-to» 13 °C and winds «less-than» 6 m/s to predict insect harassment while Brotton & Wall (1997) suggested a minimum temperature of 6 °C for oestrid fly activity. But, although he hypothesized that summer climate was responsible for differences observed among years in larval infestation levels, Nilssen (1997) has shown that cold weather certain years may affect oestrids populations very strongly. Pollard et al. (1996) found that mosquito abundance was positively correlated with temperature and negatively correlated with wind velocity and relative humidity in Alaska. Colman (2000) reported insect harassment of wild reindeer in southern Norway to be positively correlated to increasing temperature and negatively correlated with increasing cloud cover (Table 3).

Discussion

Several studies have been carried out investigating the influence of local and global weather variation on plants, and how this in turn affects population parameters of northern ungulates (Table 1). The indirect effect of climate through its impact on vegetation is confirmed through field studies showing that increased solar radiation and temperature lead to increased levels of secondary compounds in plant tissues, such as phenols and tannins, while lowering the crude protein:dry matter ratio of temperate forage plants (Jonasson et al., 1986; Laine & Henttonen, 1987; Bø & Hjeljord, 1991). The integrated effects on availability of food resources per capita, on environmental conditions and on previous reproductive success determine productivity of ungulates. Therefore, environmental conditions such as adverse weather can be a significant influence even for highly productive ungulates occurring at low densities (Adams & Dale, 1998). Van der Wal et al. (2000) suggested that selection for

plant quantity might be driven by low levels of available plant biomass and high forage quality during the growing season in the high arctic, whereas in temperate regions with high forage biomass, selection for plant quality may be of greater importance for herbivores. In Svalbard reindeer, therefore, selection for high plant biomass is likely to lead to a more favourable nitrogen and energy return than selection for high plant quality (Van der Wal et al., 2000).

Although the existence of effects of weather parameters (local and global) on ungulate population dynamics is widely accepted, there is little consensus on the direction (positive or negative) of its effects and on which variables are more important. Some of the contrasting results probably arise from methodological differences, or failure to account for other significant covariates, such as density (see e.g. Mysterud et al., 2000 and discussion above). For example, Mech et al. (1987) documented the cumulative negative effects of previous winters' snow on rates of population increase in moose and white-tailed deer. Messier (1991) analysing a smoothed version of the same dataset reported no effect of snow accumulation on population dynamics. Post & Stenseth (1998) reanalysed both original and smoothed data on dynamics of moose and white-tailed deer accounting for serial autocorrelation and using the NAO (which has a correlation with snowfall) and found that rates of increase of moose and white-tailed deer in both original and smoothed data were influenced by global climatic fluctuation at 2- and 3-year lags. However, Loison et al. (1999a) reported opposite effects of increase in spring temperature on chamois in the Alps and Pyrenees, showing different local response to the same global climatic variability at the intra-specific level using the same methodology. This suggests that contrasting responses to climate cannot be all explained by methodological problems. There is considerable biological variation in response to climate between regions, areas, and localities, between species and even within species.

Also, most studies using the NAO have not clearly shown its relationship with local weather variables of the sites actually studied. There is evidently little consensus among authors on the generalized relative importance of specific climatic variables in influencing ungulates population parameters. There is considerable regional and local variability in how ungulates respond to specific climatic variables (Klein, 1999). This demonstrates the complexity of the environmental/ecosystem relationships that also vary regionally, locally and

by species and population status (sex, age and size for example). This suggests that we should question the factors guiding choices of some specific weather variables and not others by authors in this field, as statistically it is often possible to find correlations among variables after several trials (e.g. Lindström, 1996).

A reindeer/caribou perspective

In view of their numbers and, their socio-cultural and economical importance, there is a need for studies of long time series in assessing effects of climatic variability on reindeer/caribou. Indeed, many northern indigenous peoples, including the Gwich'in of Alaska and northwestern Canada, the Inuit of Canada, Alaska and Greenland, the Sami and Komi of Fennoscandia and western Russia, and numerous other peoples of Siberia and the Russian Far East have dependence on reindeer/caribou for their livelihood. Reindeer areas in Norway experience large annual climatic variations with severe impacts on herd reproductive output, as both live and dressed weight for calves and adults vary yearly in connection with climatic variation (Reindriftsforvaltningen, 1998; R.B. Weladji & Ø. Holand, unpubl. results). Furthermore, probably to a much greater degree than other ungulates, insect harassment and associated parasitism, which is related to summer weather conditions, is of particular importance in their ecology (Mörschel & Klein, 1997; Klein, 1999; Colman, 2000). The total foraging time is considered to be a main determinant of fattening in *Rangifer* (Reimers, 1980). It is apparent that insect harassment during warm summers can have a detrimental effect on body condition and productivity of reindeer and caribou through lost foraging time, increased energy expenditure and increased parasite burden. Models investigating the effect of climate change on reindeer predict an increase in insect harassment in summer, due to an increase in average monthly temperature (Gunn & Skogland, 1997; Brotton & Wall, 1997). This may vary locally, however, because the level of harassment may vary depending on wind velocity, as insect harassment is reduced on windswept areas (Walsh *et al.*, 1992). Other factors influencing insect levels and their harassment include cloud cover (Colman, 2000), relative humidity and access to «insect relief» habitat (Pollard *et al.*, 1996; Mörschel & Klein, 1997). The effects of mosquitoes, biting flies, warble flies and nasal bot flies on reindeer and caribou may vary differentially in relation to weather conditions. This is related to the different timing of emergence

of the adult phase of these Dipteran species, their life span and their activity and flight capacities under different temperature, humidity and wind conditions (see Roby, 1978; Russel, 1993; Mörschel & Klein, 1997 above). Summer weather, through its effects on insect activity may play a detrimental role on reindeer/caribou condition during summer, temperature being a key factor. Indeed, various means have been used to investigate and evaluate the effect of insects on reindeer and caribou, and temperature has consistently appeared to play an important role in determining the level and type of avoidance behaviour of reindeer and caribou, even in the immediate absence of insects (Mörschel & Klein, 1997). The expected increased temperature with ongoing global climate change could, therefore, be more harmful for reindeer than other northern ungulates. We thus point out the limits of comparability between systems and the difficulty of generalizing about the effect of climate change broadly across northern systems, across species and even within species. The projected increased temperature in Scandinavia and other parts of the Eurasian and American North could therefore lead to increased detrimental effects on reindeer and caribou through its effect on insect activity when temperature, wind velocity and relative humidity are appropriate. The complex role of insects in the ecology of reindeer and caribou, and the associated influence of weather parameters on the ecology of these insects, renders assessment of climate variability on the population dynamics of reindeer and caribou particularly difficult. Even less is known regarding possible effects of other parasitic groups. Halvorsen *et al.* (1999) reported evidence for transmission of parasitic nematodes in Svalbard reindeer during the arctic winter. Accordingly, as global changes are predicted to affect winter climate the most, parasitic survival and transmission may increase with increased winter temperature. The relationship between climate and parasites in general should therefore be further evaluated.

The affiliation between reindeer/caribou and lichen is very strong (Boertje, 1990; Crittenden, 2000). Precipitation is one of the major processes that deliver nutrients to lichens (Crittenden, 2000). Thus, increased precipitation during winters as predicted by climate change models (Dickinson, 1986; Maxwell, 1997), may lead to improved reindeer/caribou ranges during winters. But in the presence of other plant types and under improved winter conditions, the competition edge of lichens may be reduced, leading to lichens shrinkage and to reduction of the mat-forming

lichens, which might be detrimental for reindeer and caribou.

Predictions about possible effects of the ongoing global warming cannot be made with certainty, but they will most likely be detectable, although variable between different geographic areas.

Acknowledgment

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