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The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass

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The relative importance of winter harshness and early summer foraging conditions are of prime interest when assessing the effect of global warming on artic and mountainous ecosystems. We explored how climate and vegetation onset (satellite-derived Normalized Difference Vegetation Index data) determined individual performance in three reindeer populations (data on 27 814 calves sampled over 11 years). Snow conditions, spring temperatures and topography were the main determinants of the onset of the vegetation. An earlier onset positively affected the body mass of calves born the following autumn, while there was no significant direct negative impact of the previous winter. This study underlines the major impact of winter and spring climatic conditions, determining the spring and summer food availability, and the subsequent growth of calves among alpine herbivores.

1. INTRODUCTION

Anticipating the effect of global warming in different ecosystems has become one of the major challenges for ecologists (Stenseth *et al.* 2002; Walther *et al.* 2002). Crucial for predicting future ecological responses to these global changes is a better understanding of the climatological 'downscaling process' (i.e. how the overall mean averages may change owing to local climate–topography interactions, determining the prevalent weather conditions at the scale of the plants and animals). Both mean temperature and precipitation have increased in the Northern Hemisphere (an 0.8 °C increase in the mean temperature in early spring, February to April, in the last decade has been reported; has an 8 day earlier average start of the growing season in Europe from 1989 to the present; Chmielewski & Rötzer 2002; IPCC 2001). This creates a disjunction between phenology at low and high altitude, as increased precipitation means more rain at low altitude and more snow at high altitude (Mysterud *et al.* 2001). Increased snow in mountains may create a more variable snow melt, which might be favourable to herbivores migrating from high to low altitude areas (Post & Stenseth 1999; Mysterud *et al.* 2001). However, more snow during winter may lead to more difficulties for large herbivores staying in the mountains during winter, such as alpine reindeer (*Rangifer tarandus*; Weladji 2003).

We aim to directly quantify the impact of winter climate and vegetation phenology (landscape-scale data, the Normalized Difference Vegetation Index (NDVI); Tucker *et al.* 1991) on the body mass of alpine reindeer. Reindeer calf body mass in fall is associated with over-winter survival, age at first reproduction and adult size (Gaillard *et al.* 2000).

2. MATERIAL AND METHODS

(a) *Study area*
We used data from three Saami herding districts from Sør-Trøndelag and Hedmark counties, Essand (2324 km^2), Riast/Hylling (1929 km^2) and Elgå (1007 km^2), in the middle part of Norway. The three districts are distributed within the mountainous area between 61°52′–63°28′ N and 10°55′–12°16′ E along the Swedish–Norwegian border (Weladji 2003). Essand has the largest range of altitudes (from 0 to more than 1500 m), while the two others are more homogeneous. On average, however, the smallest Elgå district in the southern edge is more elevated (around 1000 m).

(b) *Reindeer data*
We used the carcass mass of 27 814 calves slaughtered in autumn (mid-October to mid-December) between 1992 and 2002 (Essand: $n=9132$; Riast/Hylling: $n=12 401$; Elgå: $n=6281$; Weladji 2003). Reindeer density estimates in the three districts were of poor quality, but have been surprisingly stable during the study period and comparable over all years (all coefficients of variation less than 10%); which is why density has not been accounted for in the following analyses (Weladji 2003). The records are available at the Sør-Trøndelag/Hedmark Reindeer Husbandry Office in Røros, where information was also given on specific summer ranges of each population, as reindeer display migratory patterns within the study area. This information was used to determine vegetation pixels belonging to areas (see below).

(c) *Climate data*
As an index of global climate, we used the North Atlantic Oscillation (NAO; Hurrell 1995) in winter (from December to March) and in April. Local climate data were available from three meteorological stations (Selbu, station number 68340; Røros, station number 10400; and Drevsjø, station number 00700) inside the three reindeer districts. Temperatures, precipitations and snow depth were collected as monthly averages.

Correlations between local climate parameters (average temperature and sum of precipitations from December to March and the natural logarithm, the sum of snow depths from December to March plus four, and NAO indexes, were checked over the period 1992–2002 in our three districts (supplementary table 1 in Electronic Appendix). Correlations pointed in the same directions for the three districts, but none of the correlations were significant with this short time-series. Weak correlations were generally reported between local weather and the NAO indexes in Elgå. The tendency was that high NAO in winter was associated with high precipitations, high temperatures and high snow depth, while high NAO in April was related to high temperature and low precipitations. Because the NAO for year 1996 has been shown to be an outlier (Mysterud *et al.* 2001), this year was excluded from

Table 1. Parameter estimates from the LM considering NDVI—1 May from 1982 to 2001 ($R^2 = 0.18$).

parameters	estimates	s.e.	*t*-value	*p*-value
intercept	14.90	1.64	9.06	<0.001
year	−0.0005	0.0005	−1.11	0.26
latitude	−0.21	0.02	−11.03	<0.001
coast	−0.005	0.0009	−5.71	<0.001
average altitude	−0.02	0.002	−13.57	<0.001
temperature in winter	−0.003	0.001	−2.04	0.04
snow	−0.04	0.007	−5.22	<0.001
temperature in April	0.01	0.002	7.65	<0.001
precipitations in April	−0.0002	0.0001	−2.17	0.03

analyses considering NAO (supplementary tables 2 and 3 in Electronic Appendix).

(d) *Plant phenology data: the NDVI*

We used NDVI data (Tucker *et al.* 1991) collected by the National Oceanic and Atmospheric Administration satellites (http://eosdata. gsfc.nasa.gov/). The spatial scale of resolution (pixel size) is 64 km^2 and an NDVI value is available on a 10 day basis, from the 13 July 1981 to 21 September 2001.

Owing to the shape of the grazing areas, we used 18 pixels in Riast, 19 pixels in Elgå and 50 pixels in Essand. We used the NDVI value on 1 May as an index of the start of vegetation, the onset of vegetation in Europe being approximated around 23 April (Chmielewski & Rötzer 2002). In alpine areas, however, 1 May could be quite early for the vegetation onset, reducing the variability in vegetation start estimates. However, in the two other districts, 1 May was fitting for the vegetation start, and other
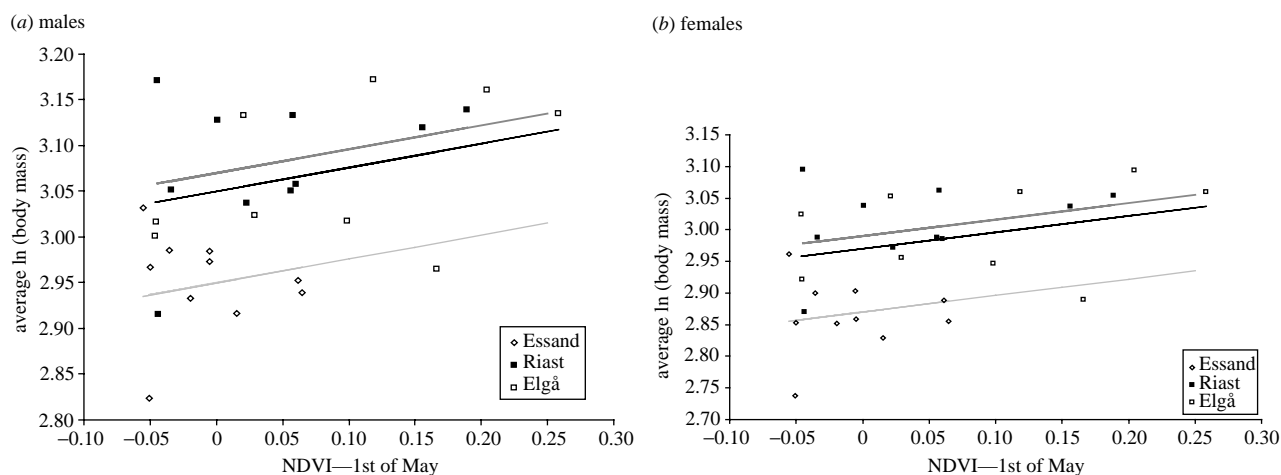

Figure 1. The relationship between average calf body mass and the vegetation onset (NDVI—1 May) in the three districts. Estimated body masses from the linear model retained are also presented for the three districts (dark grey line: Riast; black line: Elgå and light grey line: Essand).

measures (for example the NDVI slope from May to June) were highly correlated with the index on 1 May, providing a similar conclusion. Inter-annual variation in the average vegetation onset was twice greater in Riast ($-0.04 <$ NDVI < 0.19) and Elgå ($-0.04 <$ NDVI < 0.26) than in Essand ($-0.05 <$ NDVI < 0.06), but the inter-pixel variance in the vegetation start within a year was comparable between districts, except in 1999 when the differences between Elgå and Essand were marked (there was a s.d. among pixels of 0.05 in Elgå versus 0.14 in Essand).

(e) Topography data
We obtained all spatial information from the National Mapping Agency of Norway (Statens Kartverk), in a format that was used directly in a Geographical Information System (GIS; ESRI 1996). Coupling information on topography and vegetation was done through a tessellation procedure in GIS obtaining a network of 87 polygons. By using overlays, we calculated the different spatial covariates of topography for each vegetation polygon. As each NDVI polygon (8×8 km^2) is larger than each topography pixel (100×100 m^2), we calculated the average altitude of each polygon. We used the geographical longitude to estimate the distance to the coast for each vegetation pixel.

(f) Statistical analysis
We used linear models (LMs) to analyse variations in NDVI: 1 May and calf body mass, respectively. We first checked for possible nonlinearities (e.g. Mysterud *et al.* 2001), and found that the year 1996, with a very low NAO winter index (-3.78), affected parameter estimates notably (but did not qualitatively affect results), and this year was hence removed (*cf.* Mysterud *et al.* 2001).

In the NDVI model, the effects of latitude, distance to the coast, average altitude of the pixel and climatic conditions in winter and spring on the vegetation start were investigated. We considered all the available variables expected to affect vegetation onset. This first step was crucial in order to check the reliability of our remote sensing proxy, by confirming expected patterns.

In the reindeer model, covariates such as district, NAO in winter or snow and average temperature in winter, calf sex and average NDVI value on 1 May per district were included. A logarithmic transformation of body mass (ln(BM)) was used in order to obtain residuals with constant variance. In order to increase the power of our analyses, body mass averages per year, per sex and per district were considered, with previous correction for slaughtering dates. Analyses were performed in S-PLUS (Venables & Ripley 1997).

3. RESULTS
(a) NDVI, climate and topography
As expected, the vegetation generally started earlier at low altitudes, at low latitudes and near the coast. High temperature and low precipitation in the spring (positive NAO in April) were associated with advanced vegetation start. High snow depth and high temperature in winter (high NAO in winter) negatively affected the vegetation onset (table 1). Spring conditions (NAO in April) had a stronger

Table 2. Parameter estimates from the LM considering reindeer body mass from 1992 to 2002 ($R^2 = 0.58$). (Sex, districts, vegetation and winter conditions have been considered. Snow and temperature are estimated from December to March.)

parameters	estimates	s.e.	*t*-value	*p*-value
intercept	2.95	0.11	27.69	<0.001
females	-0.07	0.02	-4.47	<0.001
Riast	0.14	0.03	3.94	<0.001
Elgå	0.11	0.03	3.43	0.001
snow	0.0003	0.02	0.01	0.99
temperature in winter	0.003	0.004	0.67	0.51
NDVI	0.26	0.11	2.36	0.02

effect than winter conditions (winter NAO) on the onset of the vegetation (supplementary table 2 in Electronic Appendix).

(b) Climate, NDVI and body mass
Earlier vegetation start positively affected calf body masses (figure 1). After correcting for vegetation, no effect of snow depth, or temperature in winter on subsequent calf body mass in autumn, could be reported (table 2). There was a non-significant trend for a negative effect of winter conditions (NAO) on calf performances (supplementary table 3 in Electronic Appendix). The direct effect of winter conditions was thus weaker than the positive effect of an early vegetation start.

4. DISCUSSION
The factors influencing the onset of the vegetation in our study area are winter and spring climatic conditions and topography. Earlier vegetation onset, related in our study to higher quantity and/or quality of food resources, greatly increases population performances. The green-up phase corresponds to a highly strategically important period, allowing the calves to grow and the young deer to store enough energy to pass their first winter, a critical step in deer population dynamics (Gaillard *et al.* 2000).

There was a non-significant direct negative effect of winter conditions on calf performances after controlling for vegetation characteristics. The negative effect (Weladji 2003) of the warming trend in North European mountainous climate might be of much concern when dealing with small, protected, genetically isolated populations of reindeer. Our study clearly demonstrates that currently the direct negative impact (when calf is *in utero*) is currently less important than spring vegetation conditions, which is an old theme in deer biology (Klein 1965; Sæther & Heim 1993).

Future climatic changes have spatially contrasted effects on populations of large northern ungulates. How mountainous and artic ungulates will be able to cope with those changes (e.g. by developing adapted migration strategies) will determine their ability to maintain their presence in the most northern latitudes.

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