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Correspondence and requests for materials should be addressed to T.C.-S. (e-mail: tom.cavalier-smith@zoo.ox.ac.uk). Sequences have been deposited in GenBank under accession numbers AF165818, AJ010592 and AF083031.

Nonlinear effects of large-scale climatic variability on wild and domestic herbivores

Atle Mysterud*, Nils Chr. Stenseth*, Nigel G. Yoccoz*†, Rolf Langvatn‡ & Geir Steinheim§

* Department of Biology, Division of Zoology, University of Oslo, PO Box 1050 Blindern, N-0316 Oslo, Norway

† Department of Arctic Ecology, Norwegian Institute for Nature Research (NINA), Polar Environmental Centre, N-9296 Tromsø, Norway

‡ University Courses on Svalbard (UNIS), N-9170 Longyearbyen, Spitsbergen, Norway

§ Department of Animal Science, Agricultural University of Norway, PO Box 5025, N-1432 Ås, Norway

Large-scale climatic fluctuations, such as the North Atlantic Oscillation (NAO)^{1,2}, have been shown to affect many ecological processes^{3–6}. Such effects have been typically assumed to be linear. Only one study has reported a nonlinear relation⁷; however, that nonlinear relation was monotonic (that is, no reversal). Here we show that there is a strong nonlinear and non-monotonic (that is, reversed) effect of the NAO on body weight during the subsequent autumn for 23,838 individual wild red deer (*Cervus elaphus*) and 139,485 individual domestic sheep (*Ovis aries*) sampled over several decades on the west coast of Norway. These relationships are, at least in part, explained by comparable nonlinear and non-monotonic relations between the NAO and local climatic variables (temperature, precipitation and snow depth). The similar patterns observed for red deer and sheep, the latter of which live indoors during winter and so experience a stable energy supply in winter, suggest that the (winter) climatic variability (for which the index is a proxy) must influence the summer foraging conditions directly or indirectly.

Local weather patterns⁸ and large-scale climatic variability^{6,9–11} affect demography and population dynamics of temperate ungulates. The NAO¹ is a large-scale fluctuation in atmospheric mass between the subtropical North Atlantic region (centred on the Azores) and the subpolar North Atlantic region (centred on Iceland)¹². The NAO is positively correlated with temperature and precipitation at the west coast of Norway during winter¹. Because temperatures in this region often are around 0°C during winter, precipitation (as rain) is positively correlated and snow depth is negatively correlated with the NAO at low elevation (below 400 m), and precipitation (as snow) is positively correlated with the NAO at high elevation¹¹. Similar differential impacts of global climatic warming at low-altitude and high-altitude habitats have been reported from the Rocky Mountains¹³.

Using wild red deer (*Cervus elaphus*) and domestic sheep (*Ovis aries*) lambs as examples of wild and domestic herbivores, we have explored comparatively the effect of the NAO (being a proxy for the interannual variation in winter temperature and precipitation along the west coast of Norway^{1,11}) on individual performance (measured as body weight). As domestic sheep in Norway are free-ranging only from May/June to September/October, we can separate, through a comparison of the two species, the direct effects (costs of thermoregulation and movement in snow) and indirect effects (delayed snow melt can affect foraging conditions during summer) of winter climate.

In our study region, sheep and red deer in Norway are sympatric and have very similar diet composition and habitat use¹⁴. During winter, however, sheep are fed indoors, and as a result experience a stable interannual energy supply during that season. Thus, any relation between growth of lambs (during summer) and winter

climate must operate through indirect effects of winter climate on forage quantity and quality during summer.

A main positive effect of the NAO was found for both male and female red deer, with a plateau being reached for high NAO values (Fig. 1, Table 1). There may be direct negative effects of severe winter conditions owing to increased energetic costs of thermoregulation and locomotion; snow also reduces access to high-quality forage¹⁵. This may lead to increased loss of body mass¹⁶, retarded growth *in utero* and a delayed birth date¹⁷, which later may affect survival and fecundity of the cohort^{9,18}. High temperatures and less snow at low altitude may provide favourable winter conditions for red deer, as they descend to low elevation during the winter¹⁹.

The decreasing proportion of male calves born after winters with a decreasing NAO index is most probably due to fetal mortality *in utero* and/or perinatally¹¹, and thus is evidence for some direct effect of winter climate. There is also a clear effect of the winter NAO index

on autumn body mass of domestic sheep (Fig. 2, Table 2). Note that if there is no control for local density dependence (as in refs 6 and 9), the main positive effect of the NAO on red deer body weight will not be observed. The general positive relation between red deer body weight and the state of the NAO is reversed for the lower values of the NAO (Fig. 1), producing a nonlinear and non-monotonic response. This is the first study, to our knowledge, to report such a non-monotonic relation between the ecological performance of populations and large-scale climatic variability. The non-monotonic response of large herbivore populations to large-scale climatic variation is most probably related to a similar nonlinear and non-monotonic relationship between the NAO and local climatic variables on the west coast of Norway (Fig. 3).

As red deer and sheep showed the same response to winter climate, it is likely that it is the indirect effect of winter climate that produces the nonlinear effect. Forage quality of grasses and

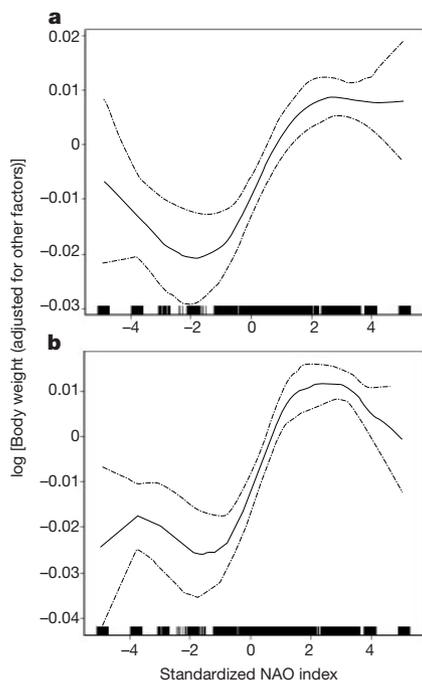


Figure 1 Relationship between autumn body weight of adult (≥ 1 yr) red deer and the North Atlantic Oscillation, an index of large-scale winter climatic variability. **a**, Female; **b**, male. Dashed lines are 95% point-wise confidence intervals. Tick marks show the locations of the observations on that variable²⁹.

Table 1 Results from fitting general additive models on variation in autumn body weight of wild red deer

	d.f.	d.f. _{spline}	F	P
Females				
NAO	1	3 versus 4	4.790	0.028
Age	1	4 versus 5	185.900	< 0.001
Density	1		3.282	< 0.001
Date of shooting	1	1 versus 2	16.701	< 0.001
Proportion of high-altitude habitat	1	4 versus 5	8.820	0.003
Degree of latitude	1	4 versus 5	6.310	0.012
Distance from the coast	1	4 versus 5	9.120	0.003
Population	4		20.290	< 0.001
Males				
NAO	1	4 versus 5	7.270	0.007
Age	1	4 versus 5	66.600	< 0.001
Density	1	2 versus 3	4.110	0.043
Date of shooting	1	4 versus 5	5.130	0.024
Proportion of high-altitude habitat	1	4 versus 5	21.470	< 0.001
Degree of latitude	1	4 versus 5	6.280	0.012
Distance from the coast	1	4 versus 5	9.570	0.002
Population	4		32.392	< 0.001

Data were from 9,175 female and 14,323 male wild red deer during the period 1965–1998.

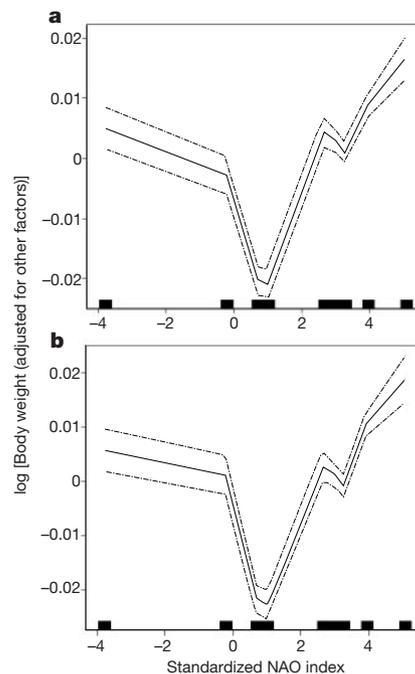


Figure 2 Relationship between autumn body weight of domestic sheep lambs, which are free-ranging only during summer, and the North Atlantic Oscillation, an index of large-scale winter climatic variability. **a**, Female; **b**, male. Dashed lines are 95% point-wise confidence intervals. Tick marks show the locations of the observations on that variable²⁹.

Table 2 Results from fitting general additive models on variation in autumn body weight of sheep

	d.f.	d.f. _{spline}	F	P
Females				
NAO	1	4 versus 5	100.66	< 0.001
Breed	1		2,264.400	< 0.001
Age of lamb	1	4 versus 5	23.204	< 0.001
Age of ewe	1	4 versus 5	60.826	< 0.001
Litter size	1	3 versus 4	5.120	0.039
Density	1	4 versus 5	49.022	< 0.001
Municipality	13		6.179	< 0.001
Males				
NAO	1	4 versus 5	118.000	< 0.001
Breed	1		1,158.100	< 0.001
Age of lamb	1	4 versus 5	11.393	< 0.001
Age of ewe	1	4 versus 5	60.654	< 0.001
Litter size	1	2 versus 3	32.222	< 0.001
Density	1	4 versus 5	57.137	< 0.001
Municipality	13		6.836	< 0.001

Data were from 71,812 female and 67,673 male sheep lambs during the period 1989–1998.

herbs declines with age (time after emergence)²⁰. Hence, it is commonly assumed that winter climate may also indirectly affect foraging conditions during summer, as deep snow may lead to an extended period of snow melt and hence a prolonged period of access to newly emergent high-quality forage^{6,10,19}. Indeed, there is an increase in variability in timing of flowering with increasing NAO index⁶. The prolonged period with access to newly emergent, high-quality forage is favourable to both red deer and sheep. Wheat quality in the UK has been positively correlated with the NAO²¹, suggesting that there may be an effect of the NAO on plant quality over and above its effect on time of emergence. Even slight changes in forage quality may substantially affect body growth of ungulates²². Our results therefore provide unambiguous support for an indirect effect of winter climate on summer foraging conditions.

A trend of increasingly warm and wet winters (as is typical for years with high NAO values) may therefore favour large herbivorous ungulates along the west coast of Norway through two separate mechanisms: first, less snow in the low-elevation wintering areas will decrease energetic costs of thermoregulation and movement, and increase access to forage in the field layer during winter¹⁰; and second, more snow in the high-elevation summer areas will lead to a prolonged period of access to high-quality forage during summer.

As body weight in ungulates is closely related to survival¹⁰, reproduction in females^{23,24} and fighting ability in males¹⁷, the population dynamical implications of the variability in the NAO

on large herbivores may be pronounced. Our result emphasizing the nonlinear and non-monotonic ecological response to large-scale climatic variability clearly demonstrates the difficulty in predicting the ecological impact of large-scale climatic fluctuations, and emphasizes the importance of routinely assessing nonlinearity in studies on global change. □

Methods

Data

The data used in this paper derive from various municipalities in six Norwegian counties: Rogaland ($n_{\text{deer}} = 6$, $n_{\text{sheep}} = 3$); Hordaland ($n_{\text{deer}} = 23$, $n_{\text{sheep}} = 3$); Sogn and Fjordane ($n_{\text{deer}} = 22$, $n_{\text{sheep}} = 4$); Møre and Romsdal ($n_{\text{deer}} = 30$, $n_{\text{sheep}} = 3$); Sør-Trøndelag ($n_{\text{deer}} = 17$, $n_{\text{sheep}} = 6$); and Nord-Trøndelag ($n_{\text{red deer}} = 7$). Data on dressed weight of 23,838 male and female red deer were sampled during the annual autumn harvest 1965–1998 (refs 9, 24). Data on covariates such as age (estimated using annuli in the cementum of the first incisor²⁵), an index for local density (total harvest in a municipality divided by the area of red deer habitat^{11,25}), date of culling^{9,25}, distance from the coast^{25,26}, degree of latitude²⁶ and proportion of high-altitude habitat²⁵ were retrieved from earlier studies.

Data on body weight, sex, breed (Dala and Spel), age of ewe (years), age of lamb (days), litter size and location (municipality) of 139,485 lambs²⁷ from 1989 to 1998 were retrieved from the Norwegian sheep recording system. These are lambs that have been free-ranging all summer, and that are weighed shortly after they are gathered from the summer pastures. The ages of ewes and lambs were known precisely, because year and date of birth had been recorded. The sheep data were extracted from the municipalities with the most red deer data. Stocking densities of sheep on pastures was calculated as total number of sheep (for each year in each municipality; known from the official agricultural statistics, Statens Kornforretning) divided by total area of the municipalities.

As an index of global winter climate we used the NAO¹, which is a large-scale fluctuation

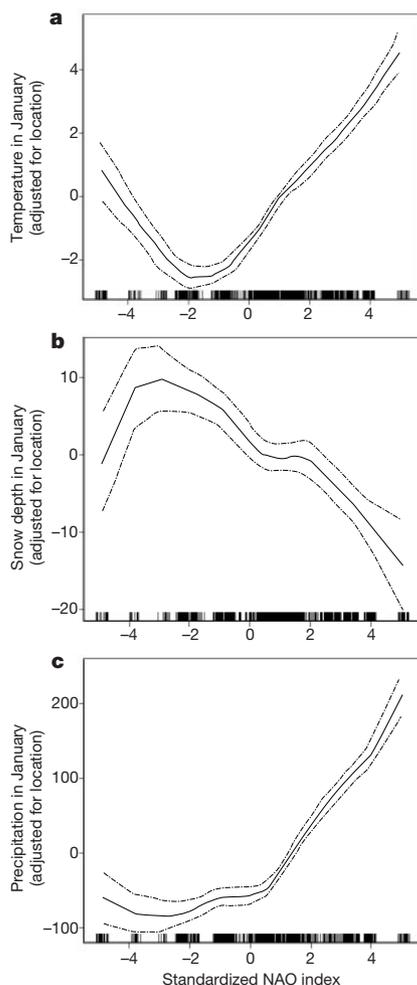


Figure 3 Relationship between the local climatic variables at the west coast of Norway and the North Atlantic Oscillation, an index of large-scale winter climatic variability.

a, Temperature (d.f. = 1, d.f._{splines} = 4 versus 5; $F = 8.100$, $P = 0.005$). **b**, Snow depth

(d.f. = 1, d.f._{splines} = 4 versus 5; $F = 9.758$, $P = 0.002$), **c**, Precipitation in January (d.f. = 1, d.f._{splines} = 4 versus 5; $F = 16.200$, $P < 0.001$). Dashed lines are 95% point-wise confidence intervals. Tick marks show the locations of the observations on that variable²⁹.

in atmospheric mass between the subtropical North Atlantic region (centred on the Azores) and the subpolar North Atlantic region (centred on Iceland)¹². The NAO index used was Hurrell's winter index¹, which is based on the difference of normalized sea level pressures between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland for the months December to March (http://goldhill.cgd.ucar.edu/cas/climind/nao_winter.html). Similar results to those reported in the main text may also be obtained by using indexes based on either the Azores (http://goldhill.cgd.ucar.edu/cas/climind/nao_monthly.html) or Gibraltar (<http://www.met.rdg.ac.uk/cag/NAO/>) as a southern station. Data on local climatic variability (temperature, snow depth and precipitation) from 1964 to 1998 on and 39 meteorological stations (restricted to stations below 250 m above sea level, as there is interaction between snow depth and altitude¹¹) were obtained from The Norwegian Meteorological Institute, Oslo.

Statistical analyses

We used general additive models (GAM) with smoothing splines^{28,29} that allow nonlinear functions of the independent variables to be chosen by the procedures, using the function GAM in the statistical package S-Plus²⁹. Splines are piecewise polynomials being smoothed (twice differentiable) in the spline knots (the control points of the splines). The complexity of the curve (that is, the number of degrees of freedom; d.f._{spline}) associated with the smoothing spline was selected by repeated fitting of the GAM with varying d.f._{spline} (1–5) for one variable, while holding d.f._{spline} of the other variables constant. The fits of the different models were then tested in an analysis of variance setting²⁹, and the selected d.f._{spline} was used in the graphical presentation (the maximum significant d.f._{spline} used). The weights of red deer and sheep were log-transformed to stabilize the variance.

For red deer, we used separate models for males and females (all ≥ 1 yr), as the response was expected to be variable among sex classes³⁰, and because interactions cannot be included in GAM²⁸. In both models for red deer, we controlled for the curvilinear effect of age and proportion of high-altitude habitat²⁵, the close to linear positive effect of distance from the coast²⁶ and degree of latitude²⁶, and the negative effect of date of culling and of local density²⁵, and the factorial variable "population"²⁵.

For sheep, we used separate models for males and females and included, in addition to the NAO, the factorial variables breed and municipality, the close to linear negative effect of litter size and density, the close to linear positive effect of age of lamb, and the curvilinear effect of age of ewe²⁷.

The lowest autumn body weights of red deer were recorded at a value of about –2 of the NAO index. Four years with a particularly low NAO value (1969, 1977, 1979 and 1996)¹ were responsible for producing this result. As sheep data (1989–1998) only contained a particularly low NAO value for 1996, the slightly different estimate for the NAO producing the lowest body weight (around NAO = 1) may be due to absence of data around a NAO index of –2. Detrending the NAO time series (by adding a smooth spline fit for 'year' to the models) did not alter the conclusion reported in the main text.

Because there is variation due to altitude, latitude and longitude¹¹, we included meteorological station as a factor variable in addition to the NAO for local climatic variability.

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Correspondence and request for material should be addressed to N.C.S. (e-mail: n.c.stenseth@bio.uio.no).

The innate immune response to bacterial flagellin is mediated by Toll-like receptor 5

Fumitaka Hayashi^{*}, Kelly D. Smith^{†‡}, Adrian Ozinsky[†], Thomas R. Hawn^{†§}, Eugene C. Yi[†], David R. Goodlett[†], Jimmy K. Eng[†], Shizuo Akira^{||}, David M. Underhill[†] & Alan Aderem[†]

^{*} Department of Immunology, [‡]Department of Pathology, [§]Division of Allergy and Infectious Diseases, University of Washington, Seattle, Washington 98195, USA

[†] Institute for Systems Biology, 4225 Roosevelt Way NE, Suite 200, Seattle, Washington 98195, USA

^{||} Department of Host Defense, Research Institute for Microbial Diseases, Osaka University, 3-1 Yamada-oka, Suita, Osaka. 565-0871, Japan

The innate immune system recognizes pathogen-associated molecular patterns (PAMPs) that are expressed on infectious agents, but not on the host. Toll-like receptors (TLRs) recognize PAMPs and mediate the production of cytokines necessary for the development of effective immunity^{1–4}. Flagellin, a principal component of bacterial flagella, is a virulence factor that is recognized by the innate immune system in organisms as diverse as flies, plants and mammals^{5–11}. Here we report that mammalian TLR5 recognizes bacterial flagellin from both Gram-positive and Gram-negative bacteria, and that activation of the receptor mobilizes the nuclear factor NF-κB and stimulates tumour necrosis factor-α production. TLR5-stimulating activity was purified from *Listeria monocytogenes* culture supernatants and identified as flagellin by tandem mass spectrometry. Expression of *L. monocytogenes* flagellin in non-flagellated *Escherichia coli* conferred on the bacterium the ability to activate TLR5, whereas deletion of the flagellin genes from *Salmonella typhimurium* abrogated TLR5-stimulating activity. All known TLRs signal through the adaptor protein MyD88. Mice challenged with bacterial flagellin rapidly produced systemic interleukin-6, whereas MyD88-null mice did not respond to flagellin. Our data suggest that TLR5, a member of the evolutionarily conserved Toll-like receptor family, has evolved to permit mammals specifically to detect flagellated bacterial pathogens.