

CLIMATIC VARIABILITY, PLANT PHENOLOGY, AND NORTHERN UNGULATES

ERIC POST¹ AND NILS CHR. STENSETH

Division of Zoology, Department of Biology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway

Abstract. Models of climate change predict that global temperatures and precipitation will increase within the next century, with the most pronounced changes occurring in northern latitudes and during winter. A large-scale atmospheric phenomenon, the North Atlantic Oscillation (NAO), is a strong determinant of both interannual variation and decadal trends in temperatures and precipitation during winter in northern latitudes, and its recent persistence in one extreme phase may be a substantial component of increases in global temperatures. Hence, we investigated the influences of large-scale climatic variability on plant phenology and ungulate population ecology by incorporating the NAO in statistical analyses of previously published data on: (1) the timing of flowering by plants in Norway, and (2) phenotypic and demographic variation in populations of northern ungulates. We analyzed 137 time series on plant phenology for 13 species of plants in Norway spanning up to 50 yr (44 ± 0.5 yr, mean ± 1 SE) and 39 time series on phenotypic and demographic traits of 7 species of northern ungulates from 16 populations in North America and northern Europe spanning up to 30 yr (18 ± 2.0 yr).

Plant phenology was significantly related to the NAO in 97 time series (71% of the total), in which dynamics of the NAO explained, on average, between 9% and 28% of the interannual variation in flowering dates. Following increasingly warm, wet winters, most plant species (9 of 13 species) bloomed earlier by an average of 13.0 ± 0.8 d to 26.4 ± 1.8 d, (mean ± 1 SE), one-third (4 of 11 species) bloomed longer by 13.4 ± 1.1 d to 18.8 ± 1.7 d, and there was an increase in spatial variability in timing of flowering across landscapes by five of six species. Woody plants displayed less sensitivity to climatic variability than did herbaceous species, and early-blooming plants were more strongly influenced by the NAO than were late-blooming plants.

Ungulate phenotypic and demographic variables were significantly related to the NAO in 28 time series (72% of the total). Large-scale climatic variability influenced growth, development, fecundity, and demographic trends of all seven species of ungulates studied, and in some populations, the NAO acted together with density dependence. Individuals within mainland populations responded to winter warming with reduced body size and increased fecundity, whereas winter warming in maritime regions led to increased body size but reduced fecundity. Across sex and age classes, between 43% and 70% of the observed range in body mass among years was attributable to the dynamics of the NAO, and within cohorts of female red deer and reindeer, 47–70% of the observed range in fecundity was related to the NAO during the winter preceding cohort birth years. All but two populations of northern ungulates declined following increasingly warmer winters, and the NAO operated, in most instances, in concert with direct density dependence to limit populations. In comparison to the original analyses of these ungulate time series, in 10 of 19 series the NAO explained an equal or greater percentage of variation than that explained by local weather. These observations indicate that large-scale climatic variability has a detectable influence on the ecology of plants and animals in a variety of terrestrial ecosystems, and that the responses of plants to winter warming may, surprisingly, be more subtle than the responses of large herbivores.

Key words: climate change; density dependence; ecosystem function; flowering dates; herbivores, large; North Atlantic Oscillation (NAO); plant–herbivore interactions; plant phenology; population dynamics; ungulates.

INTRODUCTION

Global warming is expected to produce greater increases in temperatures and precipitation during winter

than summer (Dickinson 1986, Maxwell 1997). In continental regions, it is expected to lead to heavier winter snowfall (Maxwell 1992), with the greatest changes occurring in northern latitudes (Dickinson 1986). The increase in winter temperatures may, despite greater snow accumulation, lead to earlier snow melt and a longer annual snow-free season (Maxwell 1992). Among many abiotic factors related to climate change,

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¹ E-mail: eric.post@bio.uio.no

snow depth and persistence of snow cover are important influences on the reproductive performance of plants (Galen and Stanton 1991, 1995, Inouye and McGuire 1991, Callaghan and Jonasson 1995, Jonasson et al. 1996, Molau 1996, 1997) and on growth, reproduction, and demography of large herbivores in northern latitudes (Mech et al. 1987, Albon and Clutton-Brock 1988, Hobbs 1989, Post and Stenseth 1998).

Predicted responses of plants to climatic warming derive from either experiments or observational studies incorporating local weather variables. Such responses include an earlier and longer annual season of growth (Bliss and Matveyeva 1992, Oechel and Billings 1992, Shaver and Kummerow 1992), changes in biomass production (Havström et al. 1995, Shevtsova et al. 1997), increased rates of population growth (Carlsson and Callaghan 1994), and altered timing of plant nutrient dynamics (Chapin et al. 1980). Among these, the timing and duration of growth and flowering are particularly sensitive to changes in persistence of snow cover (Galen and Stanton 1991, Inouye and McGuire 1991) and, furthermore, may be the most important factors limiting reproductive performance of northern plants (Callaghan et al. 1997, Molau 1997) and their nutritional value for herbivores (Klein 1990).

Snow depth, the duration of snow lie, and timing of snow melt also influence the foraging ecology, growth, and reproduction of northern ungulates, both directly (Watson 1971, Albon and Clutton-Brock 1988, Hobbs 1989) and indirectly through effects on timing of emergence of forage plants (Klein 1985, Jeffries et al. 1992, Post and Klein 1999). For example, snowy winters interact with landscape heterogeneity to produce spatiotemporally patchy patterns of snow melt and plant emergence (Shaver and Kummerow 1992) that prolong the availability of newly emergent, highly nutritious forage for migratory ungulates (Klein 1970, Merrill and Boyce 1991, Albon and Langvatn 1992). Furthermore, the likelihood that female red deer (*Cervus elaphus*) will conceive upon reaching sexual maturity has been linked to climate at the end of winter during their early development (Albon et al. 1987, Langvatn et al. 1996). Winter climate directly limits the abundance of northern ungulates through effects of snow or cold on survival, particularly of juveniles (Watson 1971, Clutton-Brock and Albon 1982, Mech et al. 1987, Albon and Clutton-Brock 1988, Forchhammer et al. 1998a, Gailard et al. 1998). In mainland regions, snowy winters can increase the susceptibility of ungulates to predation (Nelson and Mech 1986, Post and Stenseth 1998).

Empirical studies of the effects of large-scale climatic variability on extant biota in terrestrial ecosystems have, however, been few (e.g., Dunnett 1995, Willis et al. 1995). Traditionally, climate change studies have focused either on plants, using local weather variables (Callaghan et al. 1989, 1997, Chapin et al. 1995, Havström et al. 1995), or on animals, without data on plants (Smith et al. 1995, Post et al. 1997, Forchham-

mer et al. 1998a, b). Such studies offer little indication of how interactions between plants and herbivores will be affected by rapid climatic change (but see Brown et al. 1997, Jaksic et al. 1997). Furthermore, links between responses by vegetation to climatic change and consequent phenotypic evolution and demographic responses of ungulates, such as the changes in body size and spatial redistribution following global warming at the end of the Pleistocene (Guthrie 1982, 1984), remain speculative in the absence of long-term studies. The ecology of large-scale climatic variability is, we propose, an ongoing process that can be approached empirically by integrating ecological observations and recent developments in climatology.

The North Atlantic Oscillation and climatic variability in the Northern Hemisphere

In northern latitudes, wintertime climatic variability, defined here as both interannual fluctuation and decadal trends, is determined mainly by a large-scale alternation of atmospheric pressures called the North Atlantic Oscillation, NAO (Rogers 1984). The NAO is a meridional oscillation of atmospheric mass between Iceland and the Azores (Lamb and Pepler 1987) that has been compared to the more familiar El Niño Southern Oscillation in terms of its impact on global climate, particularly in the Northern Hemisphere (Hurrell and Van Loon 1997). Depending on where the balance of atmospheric mass lies, the NAO is either in a "high" state (mass balance over the Azores) or "low" state (mass balance over Iceland). This mass balance acts as a pressure corridor influencing the direction, magnitude, and speed of westerly winds across the Atlantic Ocean from North America to northern Europe (Fig. 1) and, thereby, wintertime temperatures and the balance of precipitation and evaporation over both continents (Rogers 1984, Lamb and Pepler 1987).

The NAO accounts for ~55% of the interannual variation in temperatures in the North Atlantic region (Schlesinger and Ramankutty 1994) and ~33% of the variation in wintertime temperatures in the Northern Hemisphere (Hurrell 1996). In Norway, fluctuations in the NAO explain up to 50% of the interannual variation in wintertime precipitation over the past 72 yr (Hurrell 1995). The NAO also exhibits phases of increase and decrease that persist over decades (Fig. 1, insert) (Hurrell 1995), and these phases, in addition to influencing the increase in average wintertime temperatures throughout much of Europe during the past two decades, may contribute to global change (Wallace et al. 1995, Dickson 1997, Hurrell and Van Loon 1997, Kerr 1997). For example, when the NAO entered a strong phase of increase in the mid-1970s, extratropical Northern Hemisphere temperatures increased by 0.21°C, which closely resembled the greenhouse warming signal predicted by some global circulation models (GCMs) (IPCC 1996). However, when the effect of the NAO was removed from this trend, the residual in-

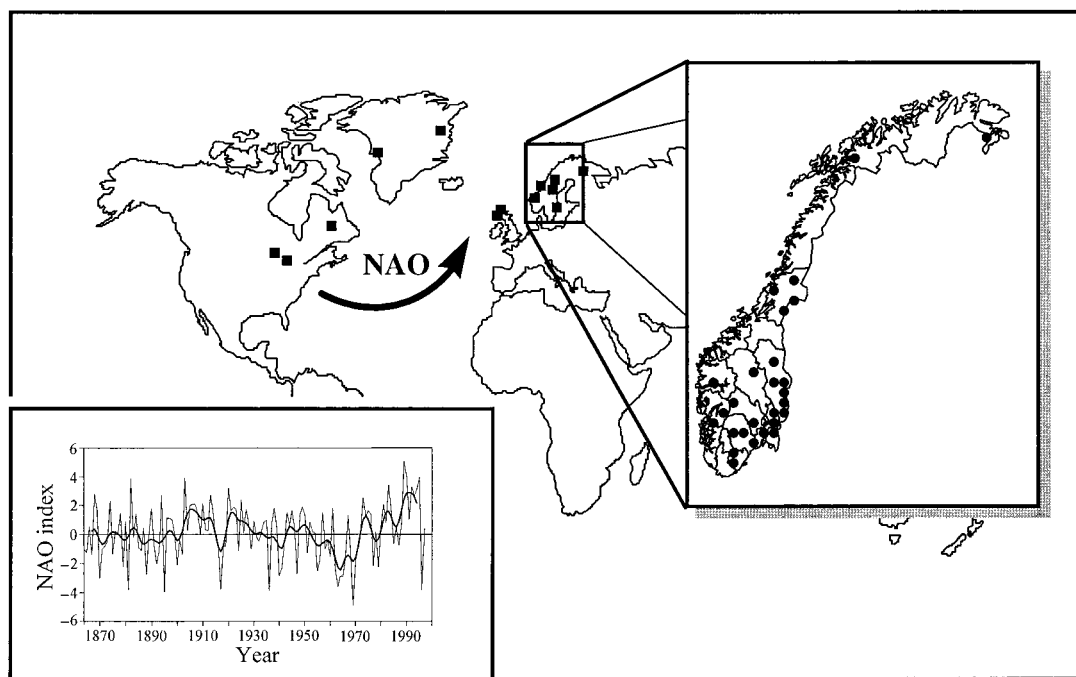


FIG. 1. The North Atlantic Oscillation (NAO) is a fluctuation in atmospheric pressures between Iceland and the Azores that determines the speed and magnitude of westerly winds from North America to northern Europe. The NAO strongly influences variation in temperatures and the balance of evaporation and precipitation during winter in Atlantic coastal North America and Europe, both interannually and on decadal time scales. Squares indicate locations of ungulate populations, and dots indicate sites of plant phenology analyzed for relationships to the NAO index. The insert depicts the NAO index (1864–1996); the heavy line is the meridional pressure gradient after smoothing with a low-pass filter to illustrate the persistence of the NAO in decadal phases (courtesy of J. Hurrell).

crease was only 0.06°C (Hurrell 1996). In the current study, we propose that an understanding of the responses by plants and herbivores to the magnitude of climatic change predicted by GCMs (Maxwell 1997) can be informed by investigating their responses to fluctuations and trends in winter climate influenced by the NAO.

MATERIAL AND METHODS

The NAO index

The state of the NAO is quantified annually during winter by the NAO index (Fig. 1, insert), which is based on the mean difference in sea level surface pressures between Stykkisholmur, Iceland, and Lisbon, Portugal, from December through March (Hurrell 1995). High, positive values of the index characterize winters with a strong westerly wind component that carries warm, moist air into northern Europe and Scandinavia, creating unusually warm, wet winters there, whereas low, negative values of the index correspond to unusually cold, dry winters in those regions (Hurrell 1995). The opposite is the case in North America and Greenland. The NAO index can be obtained from the Climate Indices website.²

² URL: <http://www.cgd.ucar.edu:80/cas/climind/>.

Plant phenology

Plant phenology data.—Lauscher and Lauscher (1990) reported annual dates of first flowering for 43 species of herbaceous and woody plants in 37 sites across Norway, and, for some species and sites, the first date on which fruit-set occurred each year, from 1928 through 1977. Sites ranged along north–south and coastal–inland gradients spanning 58°N , 7.5°E to 69.6°N , 30.4°E (Fig. 1) and elevations from 0 m above sea level (m.a.s.) to 840 m.a.s. (Table 1). We analyzed all site-specific series that contained ≥ 30 yr of data on 4–7 species, including annual dates of first flowering by *Anemone hepatica*, *A. nemorosa*, *Tussilago farfara*, *Caltha palustris*, *Calluna vulgaris*, and *Vaccinium myrtillus*, and annual dates of leaf bud burst in *Betula odorata* (Table 1); these species or genera occur in the diets of the northern ungulates that we studied (Clutton-Brock et al. 1982, Klein 1990, Albon and Langvatn 1992, Sand 1996). Our analysis included: (1) site-specific responses, and (2) temporal and spatial patterns of plant phenology.

Site-specific variation.—Responses to climatic variability by plants at a single site and interspecific differences in responses were analyzed using annual dates of first flowering at Helle, Norway (58.8°N , 9.4°E),

TABLE 1. Locations of sites on which annual dates of flowering by herbaceous plants and annual dates of leaf bud burst by *Betula odorata* were recorded in Norway from 1928 to 1977. Numbers in columns below each species refer to the number of years of data for that species at each site. Ellipses indicate lack of observation.

Site	Latitude (°N)	Longitude (°E)	Elevation (m.a.s.)†	<i>Anemone hepatica</i>	<i>Anemone nemorosa</i>	<i>Tussilago farfara</i>	<i>Caltha palustris</i>	<i>Calluna vulgaris</i>	<i>Vaccinium myrtillus</i>	<i>Betula odorata</i>
Tromsø	69.6	19.0	40	48	47	46
Jarfjordbotn	69.6	30.4	8	43	...	45	31
Trondheim	63.4	10.4	135	50	50	50	...	37	45	...
Meldal	63.2	9.9	143	...	43	47
Ranheim	63.4	10.5	43	50	50	50	45	...
Røros	62.6	11.4	840	47	47	48	48	48
Lom	61.9	8.8	631	47	...	32	...
Sel	61.8	9.5	312	37	34
Lillehammer	61.1	10.5	180	50	50	50	...	46
Øksna	60.9	11.3	203	50	50	50	50	...	30	...
Vang at Hedmark	60.8	11.2	130	50	50	50	50
Hov at Land	60.7	10.5	295	47	46	47	...	30	32	...
Hamar	60.7	11.3	127	50	50	50	50
Nesbyen	60.6	9.1	170	32	...
Morskogen	60.5	11.2	129	42	38	41
Eidsvoll verk	60.4	11.3	180	...	48	34	35	...	38	...
Grorud	60.0	10.9	180	45	45	47
Asker	59.8	10.4	78	50	50	49	46	...	42	...
Røldal	59.8	6.8	480	37	...	37	46	47
Granheim	59.7	9.9	93	36	39	43	41	36	35	...
Litlabo	59.6	5.3	30	...	48	...	43	37	39	...
Drammen	59.6	10.3	34	41	40	43	36	33	33	...
Spydeberg	59.5	11.0	115	47	49	48
Hauggrend	59.4	8.1	420	37	34
Haugesund	59.4	5.4	20	...	37	...	30	...	35	...
Notodden	59.4	9.4	58	44	50	44
Dilling	59.4	10.7	27	...	50	50	49	41
Bergstrøm	59.4	11.7	110	49	48	48
Hedrum	59.2	10.0	10	46	46	45	46
Tveit	58.3	8.1	25	47	47	50	...
Kristiansand	58.2	8.0	24	47	47	41	50	...

† Meters above sea level.

the only site for which data on several species were available for ≥ 30 yr, for the species just listed (except *B. odorata*) plus *Convallaria majalis*, *Linnaea borealis*, *Epilobium angustifolium*, *Oxalis acetosella*, *Primula officinalis*, and *Trientalis europaea*. To test for influences of climatic variability on duration of the annual season of flowering at the same site, we used data on the total number of days between onset of flowering and onset of fruiting for the following species: *Convallaria majalis*, *Tussilago farfara*, *Epilobium angustifolium*, *Caltha palustris*, *Anemone hepatica*, *A. nemorosa*, *Primula officinalis*, *Oxalis acetosella*, *Calluna vulgaris*, *Linnaea borealis*, and *Trientalis europaea*.

Temporal dynamics.—We used linear regression to test for relationships between dates of first flowering and the NAO index of the preceding winter. We adjusted degrees of freedom for tests of significance to account for autocorrelation (Bartlett 1946; see also Priestley 1981): $N' = N[(1 - a_1 a_2)/(1 + a_1 a_2)]$, in which N is the number of paired observations and a_1 and a_2 are the coefficients of autocorrelation for each of the series.

To analyze the magnitude of influence that the NAO exerted on variation in timing of flowering throughout

Norway, we quantified the number of days by which annual flowering dates varied between extreme states of the NAO, using regression equations describing relationships between flowering dates and the NAO index. For each population that exhibited significant covariation with the NAO, we used the highest and lowest values of the NAO index between 1928 and 1977 to calculate the flowering dates in those years, and took the difference between those dates as the absolute number of days by which timing of flowering differed between extremes of the NAO. We also analyzed influences of site location on the magnitude of difference in timing of flowering between the highest and lowest NAO years. For each species that displayed significant covariation with the NAO index across sites, we regressed the range of flowering dates between the highest and lowest NAO years against site latitude, longitude, and elevation (m.a.s.) in a stepwise linear analysis with alpha-to-enter and -remove set at 0.15.

To determine the influence of the NAO on the absolute number of days by which flowering season length varied, we used regression equations quantifying significant relationships between the NAO and flowering season length for species at Helle, Norway. We

used the lowest and highest values of the NAO index between 1928 and 1977 to calculate lengths of the flowering seasons in those years, and took their difference as the number of days by which the flowering season length differed between extremes of the NAO.

Spatial dynamics.—We investigated the spatial dynamics of plant phenology using dates of flowering recorded at 11–31 locations each year for: *Anemone nemorosa*, *A. hepatica*, *Calluna vulgaris*, *Vaccinium myrtillus*, *Tussilago farfara*, and *Caltha palustris*. For each species, we calculated the variance of the mean annual date of flowering across locations for each year. Subsequently, we tested for associations between annual spatial variability in dates of flowering and the NAO index of the preceeding winter, using linear regression.

Finally, to determine whether the long-term average timing of flowering by a species (“vernal” or “aestival”; Molau 1993) influenced the extent to which the NAO determined its annual dates of flowering and length of flowering, we regressed coefficients of correlation between those variables against the 50-yr mean flowering date of each species. In all regressions, we tested the assumptions of normality, linearity, and homoscedasticity using normal probability plots and plots of residuals against the independent variable (Neter et al. 1990). To remedy heteroscedasticity, we used \log_{10} -transformed dependent variables (Neter et al. 1990). All analyses were performed with SYSTAT (1992). To identify individual points that influenced the significance of regression relationships, we used the “Influence” function in SYSTAT; such points are identified in the *Results*, and we report the significance of regressions excluding these points.

Northern ungulates

Ungulate data.—We used published data on phenotypic and demographic traits from 16 populations of seven species of ungulates occurring in northern Europe, Scandinavia, and North America (Fig. 1). Data included: body mass of reindeer (*Rangifer tarandus*) calves from Finland (Kumpula and Nieminen 1992); fecundity of adult female reindeer from Norway (Skogland 1990); autumn body mass of yearling moose (*Alces alces*) from Norway (Sæther 1985) and calf, yearling, and adult moose from Sweden (Sand 1996); birth mass of red deer (*Cervus elaphus*) calves (Albon et al. 1983a) and adult mass in autumn of male and female red deer (Clutton-Brock and Albon 1983) from the Isle of Rum, Scotland (hereafter “Rum”); autumn abundance of male and female red deer (Clutton-Brock et al. 1985) and fecundity of female red deer (Clutton-Brock et al. 1985, Albon et al. 1987, Langvatn et al. 1996) from Rum; survival of red deer calves (Clutton-Brock et al. 1985) and cohort survival of yearling female red deer (Albon et al. 1987) from Rum; winter mortality (\log_e [number found dead each winter]) of male and female red deer from Rum (Clutton-Brock

and Albon 1982); autumn body mass and abundance of male and female red deer from Norway (Post et al. 1997); fecundity of female red deer from Norway (Langvatn et al. 1996); summer abundance and winter mortality of Soay sheep (*Ovis aries*) from Hirta and Village Bay, St. Kilda, UK (Clutton-Brock et al. 1991, 1992, 1997); body mass at birth of Soay sheep lambs from Village Bay (Clutton-Brock et al. 1992); summer abundance of feral goats (*Capra* sp.) on Rum (Boyd 1981); abundance of moose from Isle Royale and white-tailed deer (*Odocoileus virginianus*) from Minnesota (Messier 1991; data from Mech et al. 1987 reported therein); winter abundance of muskoxen (*Ovibos moschatus*) from East Greenland (Forchhammer and Boertmann 1993); and, finally, summer abundance of caribou (*Rangifer tarandus*) from West Greenland (Meldgaard 1986) and Quebec (Couturier et al. 1990).

Phenotypic variation.—Relationships between the NAO and phenotypic traits of northern ungulates were analyzed with linear regression in a stepwise model that allowed for simultaneous effects of density at zero and 1-yr lags and the NAO at zero to 3-yr lags. The general form of this model was

$$P_t = a_0 + \sum_d b_d X_{t-d} + \sum_k c_k \text{NAO}_{t-k} + \varepsilon_t \quad (1)$$

in which P_t is the phenotypic trait in year t or cohort t , X_{t-d} is \log_e (abundance) in the current or previous year (including all d for which $d \in [0, 1]$), NAO_{t-k} is the NAO index in the current and up to three previous winters (including all k for which $k \in [0, 3]$), and ε_t is a time-independent stochastic term with zero mean and constant variance incorporating variation not accounted for by the other parameters (Stenseth et al. 1996). For some time series, lack of published data on population density prevented inclusion of the density term in Eq. 1. We included the term “year” to remove trends from all nonstationary series. To test for the influence of density on fecundity of female red deer in Norway (reported in Langvatn et al. 1996), we used estimates of abundance from the same population reported in Forchhammer et al. (1998a). Degrees of freedom for coefficients of simple and partial correlation between each phenotypic trait and the NAO and density terms (where applicable) were adjusted for autocorrelation according to Bartlett (1946), and were considered significant at $P \leq 0.05$.

Demographic variation.—We used stepwise linear regression to analyze covariation between demographic traits (survival, mortality, and fecundity), the NAO index, and density (where overlapping data existed) using Eq. 1, letting P_t denote the demographic trait of interest. We used a separate model to analyze variation in ungulate abundance as a function of the NAO and direct density dependence by adapting a general model of population growth that included the NAO:

$$N_t = N_{t-1} \exp \left(\beta_0 + \beta_1 X_{t-1} + \sum_d \omega_{t-d} \text{NAO}_{t-d} + \varepsilon_t \right) \quad (2)$$

in which N_t denotes abundance in year t , N_{t-1} denotes abundance in the previous year, X_{t-1} denotes $\log_e(\text{abundance})$ in year $t-1$, NAO_{t-d} is the NAO index in the current and up to three previous winters (including all d for which $d \in [0, 3]$), and ε_t has the same properties as in Eq. 1. This model (Eq. 2) assumes a log-linear relationship between population growth rate and abundance known as the Gompertz (1825) assumption, which has been favored in models of population dynamics because of its close approximation to biological processes such as fecundity and survival that are nonlinearly related to density (Royama 1992, Bjørnstad et al. 1995, Stenseth et al. 1996). This scenario is biologically plausible for ungulates (Clutton-Brock et al. 1997, Forchhammer et al. 1998a). Eq. 2 can be expressed as linear-additive on a log scale (cf. Forchhammer et al. 1998a):

$$X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \sum_d \omega_{t-d}\text{NAO}_{t-d} + \varepsilon_t \quad (3)$$

in which X_t is $\log_e(\text{abundance})$ in year t , X_{t-1} is $\log_e(\text{abundance})$ in the previous year, and NAO_{t-d} and ε_t are the same as described for Eq. 2. Eq. 3 is thus an autoregressive model of the influences of direct density dependence and the NAO on variation in ungulate abundance. Because the coefficient of direct density dependence includes the value "one" (due to the log scale), its significance was tested as being different from one with a two-tailed t test (cf. Bjørnstad et al. 1995): values less than one indicate negative, direct density dependence, and values greater than one indicate positive, direct density dependence. Nonstationary series were detrended by including "year" in the regression, because regression between two series that are linearly related to time can give spurious results (Royama 1992). Tests for significance of coefficients of simple and partial correlation from stepwise regression were adjusted for autocorrelation according to Bartlett (1946).

Absolute and relative differences between extremes of the NAO.—To quantify the absolute amount by which mass and fecundity differed between extremes of the NAO, we used regression equations from populations displaying significant covariation with the NAO. We used the highest and lowest values of the NAO index observed during the period for which body mass and fecundity were recorded, and used the relevant regression equations to calculate mass and fecundity for those years. The difference between these was the range of values occurring between extremes of the NAO. This difference was compared to the total observed range of body mass and fecundity for each population: the percentage of the total observed range that composed the range attributable to variation between extremes of the NAO was the division of the latter by the former.

Relations between plant phenology, red deer fecundity, and the NAO.—To determine the direct influence

of plant phenology on fecundity of red deer, we regressed fecundity of red deer cohorts (Langvatn et al. 1996) against: (1) timing of flowering in cohort birth years, and (2) spatial variability in timing of flowering in cohort birth years. We used data for plant species occurring within the range of the population of red deer in Norway for which fecundity data were published, including *Tussilago farfara*, *Anemone nemorosa*, and *A. hepatica* for the cohort birth years 1968–1977. All regressions were performed with SYSTAT (1992), with the diagnostic procedures for normality, linearity, homoscedasticity, and influential points as previously described for the plant analyses.

Effects of the NAO vs. local weather.—Finally, as a qualitative assessment of the importance of the NAO vs. local weather in determining variation in phenotypic and demographic traits of northern ungulates, we compared the proportion of the total variance in these traits explained by the NAO with the proportion explained by local weather in the original studies. This comparison was only possible where correlations with local weather were reported. We considered r values to be different when their difference equaled or exceeded 0.10, and to be equal when their difference was less than 0.10.

RESULTS

Plant responses

Plants bloomed earlier following positive NAO (warm, wet) winters. Dates of flowering by *Anemone hepatica*, *A. nemorosa*, *Tussilago farfara*, and *Caltha palustris* were negatively related to the NAO index on most sites (Table 2). The median percentage of variation in annual dates of flowering that was explained by the NAO index was 28% for *Anemone hepatica*, 18% for *A. nemorosa*, 19% for *Tussilago farfara*, and 9% for *Caltha palustris*. Woody plants were less responsive to fluctuations in the NAO: flowering by *Calluna vulgaris* and *Vaccinium myrtillus*, and leaf emergence by *Betula odorata*, covaried with the NAO on less than half of the sites (Table 2). From 1928 until 1977, the lowest and highest values of the NAO index were -4.76 (1969) and 2.18 (1973). The mean (± 1 SE) number of days by which timing of flowering differed between these values was: *Anemone nemorosa*, 19.7 ± 1.5 d; *A. hepatica*, 26.4 ± 1.8 d; *Tussilago farfara*, 25.5 ± 1.1 d; *Vaccinium myrtillus*, 15.5 ± 1.6 d; and *Caltha palustris*, 13.0 ± 0.8 d.

Timing of flowering (see Fig. 2) varied with the NAO more strongly in southern than in northern Norway (for *Anemone nemorosa*, *A. hepatica*, and *Vaccinium myrtillus*), and at lower elevations (for *Tussilago farfara*). Correlations between flowering dates of *Caltha palustris* and the NAO were unrelated to latitude ($F = 0.67$, $P > 0.05$), longitude ($F = 0.14$, $P > 0.05$), and elevation ($F = 0.93$, $P > 0.05$). Neither *Calluna vulgaris* nor *Betula odorata* displayed sufficient covariation

TABLE 2. Coefficients of simple correlation between the North Atlantic Oscillation (NAO) index and annual dates of flowering by herbaceous plants and annual dates of leaf bud burst by *Betula odorata* in Norway from 1928 to 1977.

Site	<i>Anemone hepatica</i>	<i>Anemone nemorosa</i>	<i>Tussilago farfara</i>	<i>Caltha palustris</i>	<i>Calluna vulgaris</i>	<i>Vaccinium myrtillus</i>	<i>Betula odorata</i>
Tromsø	-0.24	-0.04	-0.17
Jarfjordbotn	-0.13	...	-0.07	0.07
Trondheim	-0.36	-0.26	-0.37	...	0.10	0.09	...
Meldal	...	-0.33	-0.49
Ranheim	-0.53	-0.48	-0.41	-0.19	...
Røros	-0.24	-0.01	-0.04	0.03	0.08
Lom	-0.01	...	-0.01	...
Sel	-0.20	-0.35
Lillehammer	-0.35	-0.14	-0.14	...	0.26
Øksna	-0.55	-0.34	-0.46	-0.28	...	-0.17	...
Vang at Hedmark	-0.71	-0.52	-0.59	-0.55
Hov at Land	-0.42	-0.13	-0.24	...	0.03	0.04	...
Hamar	-0.44	-0.34	-0.44	-0.29
Nesbyen	-0.41	...
Morskogen	-0.40	-0.35	-0.45
Eidsvoll verk	...	-0.41	-0.32	-0.40	...	-0.13	...
Grorud	-0.57	-0.59	-0.43
Asker	-0.54	-0.46	-0.53	-0.35	...	-0.43	...
Røldal	-0.30	...	0.20	-0.003	-0.24
Granheim	-0.41	-0.34	-0.44	-0.26	-0.13	-0.31	...
Litlabo	...	-0.28	...	-0.29	0.10	-0.39	...
Drammen	-0.55	-0.61	-0.51	-0.30	-0.07	-0.34	...
Spydeberg	-0.52	-0.51	-0.51
Hauggrend	-0.56	-0.34
Haugesund	...	-0.23	...	-0.39	...	-0.25	...
Notodden	-0.50	-0.43	-0.51
Dilling	...	-0.46	-0.50	-0.34	0.16	-0.36	...
Bergstrøm	-0.55	-0.46	-0.50
Hedrum	-0.43	-0.50	-0.43	-0.39	...	-0.50	...
Tveit	-0.53	-0.53	-0.56	...
Kristiansand	-0.61	-0.61	-0.21	-0.60	...

Notes: Boldface type indicates significance ($P \leq 0.05$). Ellipses indicate that data were lacking.

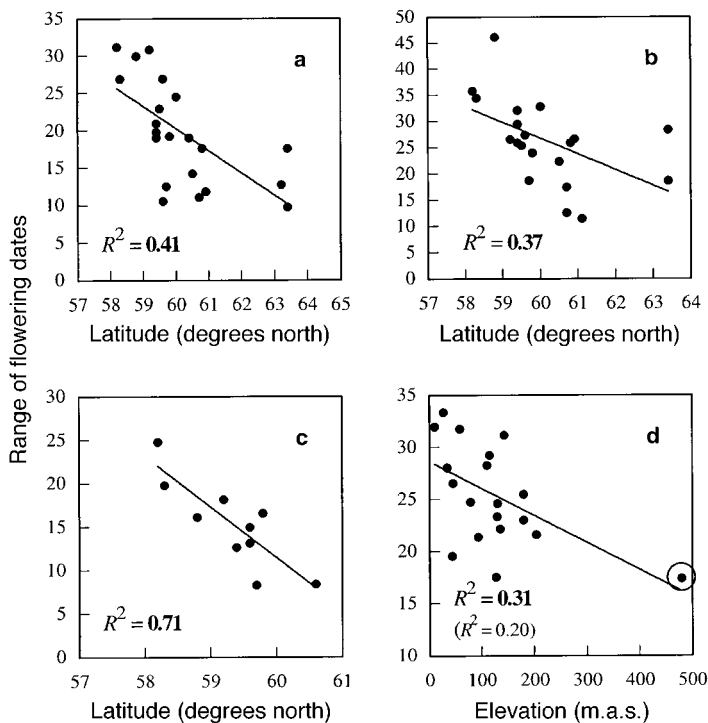


FIG. 2. The number of days by which the annual timing of flowering by (a) *Anemone nemorosa*, (b) *A. hepatica*, (c) *Vaccinium myrtillus*, and (d) *Tussilago farfara* varied between extreme states of the North Atlantic Oscillation in Norway from 1928 to 1977, as influenced by latitude (a–c) and elevation (d), in meters above sea level. In (d), the circled point influenced the regression; the value in parentheses is the coefficient of determination when the point is excluded. Boldface type for R^2 values indicates significance ($P \leq 0.05$).

TABLE 3. Site-specific responses of plants to climatic variability indicated by coefficients of simple correlation between the North Atlantic Oscillation (NAO) index and (1) annual dates of flowering and (2) duration of the annual flowering season by plants occurring at Helle, Norway (58.8° N, 9.4° E), 1928–1977.

Species	Flowering dates		Flowering season length	
	<i>r</i>	<i>n</i> (yr)	<i>r</i>	<i>n</i> (yr)
<i>Anemone hepatica</i>	−0.60	50	0.26	38
<i>Anemone nemorosa</i>	−0.60	50	0.25	38
<i>Convallaria majalis</i>	−0.52	50	0.43	37
<i>Linnaea borealis</i>	−0.45	44	0.001	30
<i>Epilobium angustifolium</i>	−0.44	49	0.29	38
<i>Tussilago farfara</i>	−0.43	50	0.37	42
<i>Vaccinium myrtillus</i>	−0.43	50
<i>Caltha palustris</i>	−0.40	49	0.28	38
<i>Oxalis acetosella</i>	−0.38	47	0.12	33
<i>Primula officinalis</i>	−0.34	45	0.19	37
<i>Trientalis europaea</i>	−0.17	47	−0.14	31
<i>Calluna vulgaris</i>	0.05	49	0.02	37

Notes: Boldface type indicates significance ($P \leq 0.05$). Ellipses indicate that data were lacking.

with the NAO index to warrant an investigation of the influences of site location.

At Helle, Norway, timing of flowering by 10 of 12 species was negatively related to the NAO index (Table 3). The flowering season for 4 of 11 species at Helle

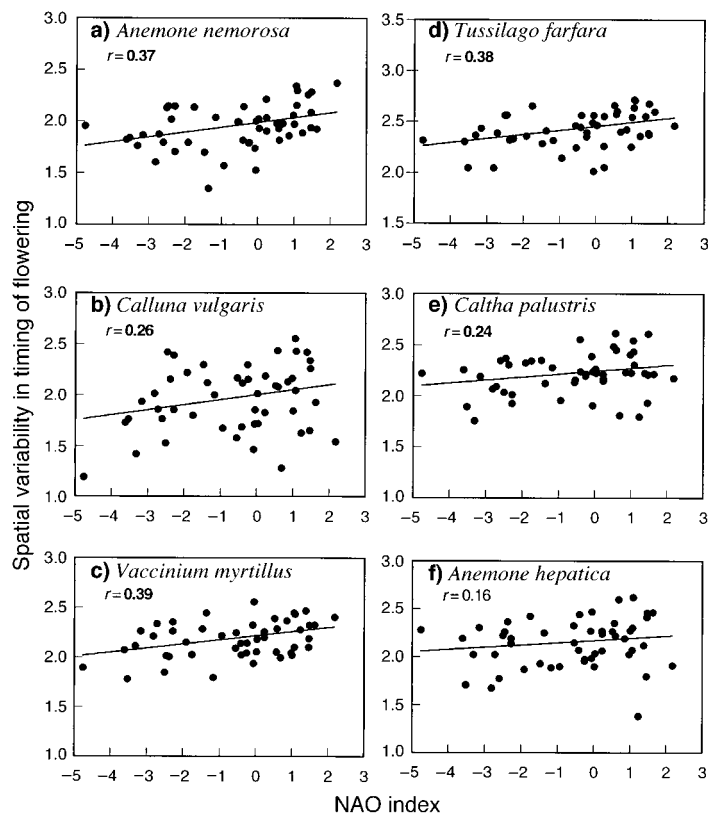
was prolonged following warm, wet winters (Table 3) by 18.8 ± 1.7 d (mean ± 1 SE) for *Anemone hepatica*, 17.1 ± 1.4 d for *Epilobium angustifolium*, 18.5 ± 1.1 d for *Tussilago farfara*, and 13.4 ± 1.1 d for *Caltha palustris*. Within years, the spatial variability of timing of flowering across sites increased with the NAO index for *Anemone nemorosa*, *Calluna vulgaris*, *Vaccinium myrtillus*, *Tussilago farfara*, *Caltha palustris*, and, marginally, *Anemone hepatica* (Fig. 3).

Finally, early-blooming plants were more strongly influenced by the NAO than late-blooming plants (Fig. 4). Similarly, the length of flowering by early-blooming plants exhibited a greater degree of correlation with the NAO index than did the length of flowering by late-blooming plants (Fig. 4).

Ungulate responses: eastern Atlantic

Body mass and fecundity of ungulates east of the Atlantic varied with the NAO index in contrasting fashion in mainland and maritime regions. In Norway, red deer born following positive NAO (warm, wet) winters were smaller as adults than were those carried in utero during negative NAO (cold, dry) winters (Table 4). On Rum, in contrast, birth mass and adult mass of red deer increased following positive NAO (warm, wet) winters. Although birth mass of red deer calves correlated with the NAO index of the winter in which they were in utero, autumn mass of adult male red deer correlated

FIG. 3. Increases in the spatial variance of the mean annual date of first flowering (1928–1977) across sites in Norway in relation to the North Atlantic Oscillation (NAO) by (a) *Anemone nemorosa*, (b) *Calluna vulgaris*, (c) *Vaccinium myrtillus*, (d) *Tussilago farfara*, (e) *Caltha palustris*, and (f) *Anemone hepatica*. Each point represents the variance of the mean date of first flowering across all sites on which a species occurred (log₁₀-transformed to remedy heteroscedasticity; sample sizes are reported in Table 1), plotted against the NAO index of the preceding winter. Boldface type for *r* indicates significant correlations ($P \leq 0.05$). For *Anemone hepatica*, $P = 0.06$.



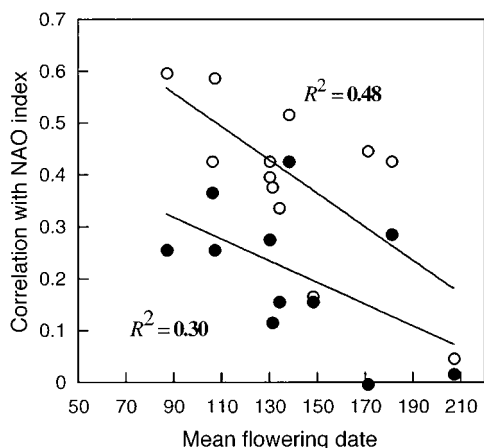


FIG. 4. Relationships between 50-yr mean flowering dates of plants at Helle, Norway, and the degree of correlation between the North Atlantic Oscillation (NAO) index and (1) annual date of first flowering (open circles) and (2) length of the annual flowering season (solid circles). The 50-yr mean flowering date (x-axis) for each species is the average Julian date on which the species first flowered between 1928 and 1977. Both regressions are significant ($P \leq 0.05$).

with the NAO index of the previous winter. In Norway, female red deer were more likely to produce calves at the age of first reproduction if they were born following positive NAO winters. In contrast, fecundity of female red deer on Rum correlated negatively with the NAO index of the winter in which they were in utero. Yearling moose in Norway were heavier if born following positive NAO winters, but body mass of moose in Sweden, where wintertime climate was more continental (Sand 1996) declined following warm, wet winters. In the maritime region of Village Bay (Hirta), Soay sheep lambs were born lighter following positive NAO (warm, wet) winters. Finally, fecundity of female reindeer in Norway declined 1 yr after warm, wet winters. Only fecundity of red deer hinds on Rum and birth mass of Soay sheep in Village Bay were significantly related to density (Table 4).

Abundance of ungulates on ranges east of the Atlantic varied with the NAO index in contrasting fashion in mainland and maritime regions (Table 5). On the mainland, autumn abundance of adult male and female red deer in Norway increased 2 yr after positive NAO winters. In contrast, autumn abundance of adult male red deer on Rum, and of Soay sheep on St. Kilda, declined following positive NAO winters. Abundance of female red deer on Rum, in contrast, increased 2 yr after warm, wet winters. In addition to being born larger, female red deer on Rum that were carried in utero during positive NAO winters were also more likely to survive as yearlings. As adults, however, male and female red deer on Rum suffered increased mortality 1 yr after positive NAO winters. Winter mortality of Soay sheep lambs was unrelated to the NAO, but displayed strong density dependence. Abundance of feral goats

on Rum declined 1 yr after warm, wet winters. Density dependence acted together with the NAO to limit abundance of Soay sheep on Hirta and in Village Bay, and feral goats on Rum, but was not significant for male or female red deer on Rum (Table 5).

Body mass of northern ungulates varied over a range of 1.5–22.5 kg, depending on species and age class (Fig. 5). The range of body mass between extremes of the NAO index was, on average, $56.3 \pm 0.03\%$ of the total observed range. Thus, although the absolute amount by which mass varied with the NAO was never greater than 1–2 kg for juveniles and 10–12 kg for adults, within each population the difference between extremes of the NAO was between 43% and 70% of the total amount by which they were observed to differ (Fig. 5). Similarly, within populations and age classes, fecundity of northern ungulates varied between 30% and 90% (Fig. 5), but the range of fecundity attributable to variation between extremes of the NAO was between 47% and 70% of the overall range of values.

Ungulate responses: western Atlantic

Muskoxen in Greenland declined 1 yr after low NAO (warm, wet) winters, as did caribou in the Sisimiut herd of West Greenland (Table 5). Moose on Isle Royale declined 2 yr after low NAO (warm, wet) winters, and white-tailed deer in Minnesota declined 3 yr after low NAO winters. All populations west of the Atlantic Ocean displayed significant, negative density dependence, the strongest occurring in white-tailed deer in Minnesota (Table 5).

Relationships between plant phenology and fecundity of red deer

In Norway, red deer born in years of early flowering were between 15% and 25% more likely to produce calves as 2-yr-olds than were red deer born during years of late flowering (Fig. 6a–c, e–g). Furthermore, female red deer born during years when the spatial variability of flowering was high were ~25% more likely to calve as 2-yr-olds than were those born during years when there was little spatial variability in timing of flowering (Fig. 6d, h). During red deer birth years 1968–1977, the NAO accounted for 33–47% of the variation in flowering dates and 24% of the spatial variation in flowering (Fig. 6e–h).

Influences of the NAO and local weather

The NAO explained as much or more of the variance in phenotypic traits as did local weather in 5 of 10 time series (Table 4). For demographic traits, the NAO explained more of the variance than did local weather in 5 of 9 series (Table 5).

DISCUSSION

Temporal and spatial dynamics of plant phenology

The timing of snowmelt is a major determinant of emergence phenology (Inouye and McGuire 1991, Ga-

TABLE 4. Coefficients of simple correlation between phenotypic traits of northern ungulates and the North Atlantic Oscillation (NAO) index.

Species	Location	Trait†	n (yr)	NAO‡	Density	Winter season	NAO vs. local§
Reindeer	Finland	calf mass ^a	13	(-0.38)	...	in utero	<
	Norway	adult female fecundity ^b	11	-0.51	...	1 yr previous	
Moose	Norway	yearling mass, south ^c	20	0.59	...	in utero	<
		yearling mass, north ^c	14	0.46	...	in utero	<
	Sweden	calf mass ^d	13	-0.72	(0.33)	3 yr previous	>
		yearling mass ^d	13	-0.48	(0.09)	3 yr previous	>
		adult female mass ^d	13	-0.61	(0.29)	3 yr previous	>
		adult male mass ^d	13	(-0.32)	(0.25)	3 yr previous	
Red deer	Rum	adult male mass ^e	20	(0.01)	...	in utero	
		adult female mass ^e	20	0.66	(0.12)	previous	
				0.34	...	in utero	
		male calf birth mass ^f	9	(0.12)	-0.34	previous	
		female calf birth mass ^f	13	0.68	(0.09)	in utero	=
		cohort fecundity (3-yr-olds) ^g	21	0.65	(0.19)	in utero	
		cohort fecundity (milk hinds) ^h	15	-0.46	-0.70	in utero	<
		cohort fecundity (yeld hinds) ^h	16	-0.67	0.44	in utero	
		adult female mass ⁱ	28	(0.18)	(-0.01)	in utero	
		adult male mass ⁱ	28	-0.36	...	in utero	
Soay sheep	Village Bay	cohort fecundity (2-yr-olds) ^g	20	(-0.32 ^j)	...	in utero	
			20	0.64	(-0.11)	in utero	>
		lamb birth mass ^j	6	-0.98	-0.90	in utero	

Notes: Where data were available, the effect of density dependence on phenotypic variation was included in a stepwise multiple regression. The column "winter season" refers to the lag of the NAO term. Boldface type indicates significance ($P \leq 0.05$), with degrees of freedom adjusted for autocorrelation; parentheses indicate lack of significance due to failure of the term to enter the model. Lightface entries without parentheses indicate that the term entered the model but was nonsignificant after adjusting for autocorrelation. Ellipses indicate that density estimates were not available; blank cells indicate that a direct comparison was not possible.

† Key to references: ^a Kumpula and Nieminen (1992), ^b Skogland (1990), ^c Sæther (1985), ^d Sand (1996), ^e Clutton-Brock and Albon (1985), ^f Albon et al. (1983), ^g Langvatn et al. (1996), ^h Albon et al. (1987), ⁱ Post et al. (1997), and ^j Clutton-Brock et al. (1992).

‡ Partial correlation between the trait and the NAO index when the partial correlation with density was included.

§ Symbols indicate whether the NAO explained more (>), less (<), or an equal (=) percentage of the variance in the dependent variable compared to local weather.

len and Stanton 1995, Walker et al. 1995) and, thereby, flowering phenology and reproductive success in northern plants (Dieringer 1991, Galen and Stanton 1991, Molau 1996). In this study, 11 of 13 species bloomed earlier (Table 2) by 13–26 d following warmer, wetter winters, presumably because warm temperatures in positive NAO winters led to earlier snowmelt, or, on the coast, less snow accumulation. Additionally, one-third of the species bloomed longer (Table 3) by 13–19 d, and the spatial variability of flowering by five of six species increased following warm winters (Fig. 3). Forbs were more responsive to large-scale climatic variability than woody plants, and the effects of the NAO on plant phenology were more pronounced at southern than at northern latitudes (Fig. 2).

Responses of plants to the NAO were, however, slight compared to plant responses to local weather in other studies. For example, local weather explained 65% of the variation in flowering dates of *Anemone nemorosa* and 60% of the variation in dates of leaf bud

burst in *Betula* sp. in the United Kingdom (Sparks and Carey 1995). Nonetheless, plants in this study responded to variation in a single atmospheric phenomenon over a diverse array of sites and local weather regimes. Moreover, the number of days by which flowering differed between the coldest and warmest NAO winters (on average, 13–26 d) is probably of biological significance for northern plants. An advance of 15–28 d in onset of flowering can, for example, significantly increase the number of flowers produced, the number and size of seeds, and the survival of seedlings (Schmitt 1983, Galen and Stanton 1991, Molau 1996). Similarly, prolongation of the flowering season on the scale that we observed in response to the NAO (between 13 and 19 d) enhanced flower production, seed set, and seedling recruitment in other studies (Schmitt 1983, Walker et al. 1995).

The greater response of plants to the NAO at southern latitudes and low elevations (Fig. 2) contrasts with previous observations of greater plant responses to

TABLE 5. Coefficients of simple correlation between demographic traits of northern ungulates and the North Atlantic Oscillation (NAO) index, in populations (a) east and (b) west of the Atlantic Ocean.

Species	Location	Trait†	n (yr)	NAO‡	DD§		Winter season	NAO vs. local¶
					r	(1 + β ₁) ± 1 SE		
a) East of the Atlantic								
Red deer	Rum	adult male abundance	13	−0.52	...	0.63 ± 0.24	previous	
		adult female abundance	14	0.70	...	1.06 ± 0.06	2 yr previous	
		calf winter mortality	13	(0.23)	(−0.04)	...	current	<
		calf summer mortality ^a	13	(0.41)	(0.07)	...	in utero	<
		yearling survival ^b	16	0.58	−0.46	...	in utero	>
		adult male winter mortality ^c	11	0.79	(−0.17)	...	1 yr previous	>
		adult female winter mortality ^c	11	0.75	(−0.30)	...	1 yr previous	>
	Norway	adult male abundance ^d	30	0.51	2 yr previous	
		adult female abundance ^d	30	0.46	2 yr previous	
Soay sheep	Hirta	abundance ^e	13	−0.78	...	−0.14 ± 0.14	previous	
				−0.80	...		3 yr previous	
	Village Bay	abundance ^e	16	−0.49	...	−0.31 ± 0.24	previous	
		male lamb winter mortality ^f	6	−0.67	0.88	...	1 yr previous	
		female lamb winter mortality ^f	6	−0.61	0.81	...	current	
Feral goats	Rum	abundance ^g	16	−0.75	...	0.37 ± 0.27	1 yr previous	>
b) West of the Atlantic								
Moose	Isle Royale	abundance ^h	18	0.45	...	0.63 ± 0.17	2 yr previous	<
Muskox	East Greenland	abundance ⁱ	28	0.38	...	0.21 ± 0.19	1 yr previous	<
Caribou	West Greenland							
	Sisimiut	abundance ^j	22	0.36	...	0.67 ± 0.15	previous	
	Pamiut	abundance ^j	72	(0.24)	...	0.65 ± 0.09	1 yr previous	
	Quebec	abundance ^k	8	(0.49)	1 yr previous	
White-tailed deer	Minnesota	abundance ^h	11	0.83	...	−0.14 ± 0.23	3 yr previous	>

Notes: Where data were available, the effect of density dependence was included as a direct autoregressive term in stepwise multiple regression. All nonstationary series were detrended by including the term "year" in the regression. Boldface type indicates significance ($P \leq 0.05$), with degrees of freedom adjusted for autocorrelation; parentheses indicate lack of significance due to the failure of the term to enter the model; plain type without parentheses indicates that the term entered the model, but was nonsignificant after adjusting for autocorrelation.

† Key to references: ^a Clutton-Brock et al. (1985), ^b Albon et al. (1987), ^c Clutton-Brock and Albon (1982), ^d Post et al. (1997), ^e Clutton-Brock et al. (1991), ^f Clutton-Brock et al. (1992), ^g Boyd (1981), ^h Messier (1991), ⁱ Forchhammer and Boertmann (1993), ^j Meldgaard (1986), and ^k Couturier et al. (1990).

‡ Coefficient of partial correlation between the trait and the NAO index after accounting for variation due to density dependence (the coefficient of partial correlation with density is given as r under the heading DD).

§ Ellipses indicate that density was not included in the regression, whereas the term $(1 + \beta_1)$ is the coefficient of direct density dependence from models of abundance.

|| This refers to the lag of the NAO term(s).

¶ This indicates whether the NAO explained more (>) or less (<) of the variance in the dependent variable than did local weather. Blank cells indicate that a direct comparison was not possible.

temperature and nutrient manipulations at the northernmost extent of their distribution or in harsh environments (Wookey et al. 1993, Jonasson et al. 1996). Phenotypic plasticity to environmental perturbation may, however, be reduced in northern latitudes where harsh environments induce intense selective pressures (Fetcher and Shaver 1990). Additionally, our observations may simply reflect less influence of the NAO on local weather in northern latitudes and high elevations. The slight response by shrubs to the NAO contradicts previous observations of strong phenological and growth responses of shrubs to manipulations simulating climatic change (Jonasson et al. 1996). Instead, our results seem to corroborate the results of

Chapin and Shaver (1996), who observed that slow-turnover, woody plants were less responsive to simulated climatic change; in our study, *Calluna vulgaris*, *Vaccinium myrtillus*, and *Betula odorata* were less responsive to the NAO than were forbs.

In addition to influences of latitude and elevation, the long-term average flowering date of a species moderated its sensitivity to climatic variability: vernal species displayed greater response to the NAO than did late-aestival species (Fig. 4), perhaps because early-flowering species tend to be more variable in their timing of flowering and, thus, more susceptible to variation in climate in late winter (Fitter et al. 1995). The conservative strategy of blooming late may buffer a species

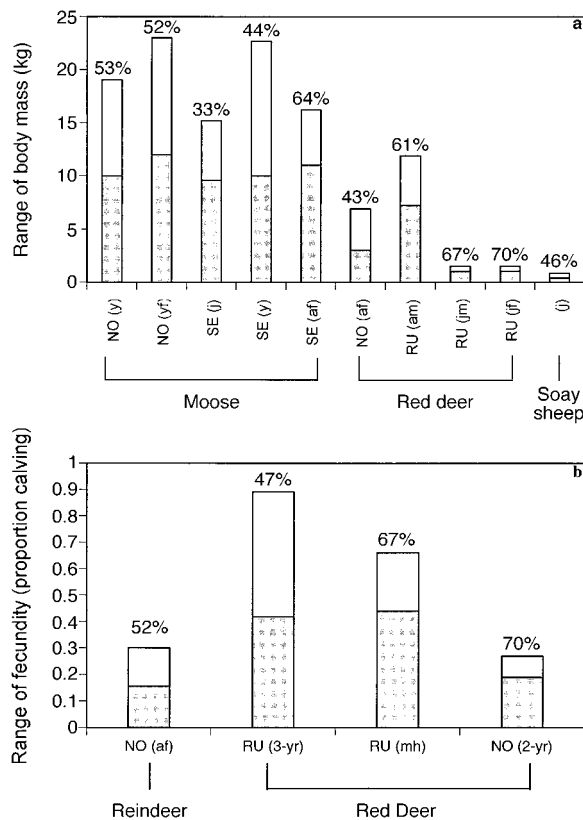


FIG. 5. Observed ranges of (a) body mass (kg) and (b) fecundity (proportion calving) reported for northern ungulates that displayed covariation in these traits with the North Atlantic Oscillation (NAO) index. Categories in (a) and (b) are: NO, Norway; SE, Sweden; and RU, Rum, Scotland. Abbreviations in (a): j, juvenile; y, yearling; a, adult; f, female; and m, male. Abbreviations in (b), 3-yr, three-year-old; mh, milk hind; and 2-yr, two-year-old. The shading in each bar depicts the range of body mass or fecundity observed between extremes of the NAO index, and the value above each bar is the percentage of the total observed range that occurred between extremes of the NAO index.

against interannual climatic extremes at the beginning of the growth season (Molau 1993), but may, at the same time, leave such species out-competed by early-blooming species that capitalize on rapid emergence following warm winters (Grime et al. 1993, Molau 1997).

The increase in spatial variability of flowering following warm winters (Fig. 3) is, we propose, due to the interaction between snow and landscape heterogeneity. In Norway, snow cover tends to persist longer with increasing elevation and latitude (Langvatn and Albon 1986), and perhaps also with increasing distance from oceanic coasts (Albon and Langvatn 1992). Thus, following snowy winters, plant phenology is delayed along those same gradients (Fig. 2). That this reflects interactions between landscape and climate, rather than a phenotypic response by plants, is suggested by the association between the NAO index and variability of

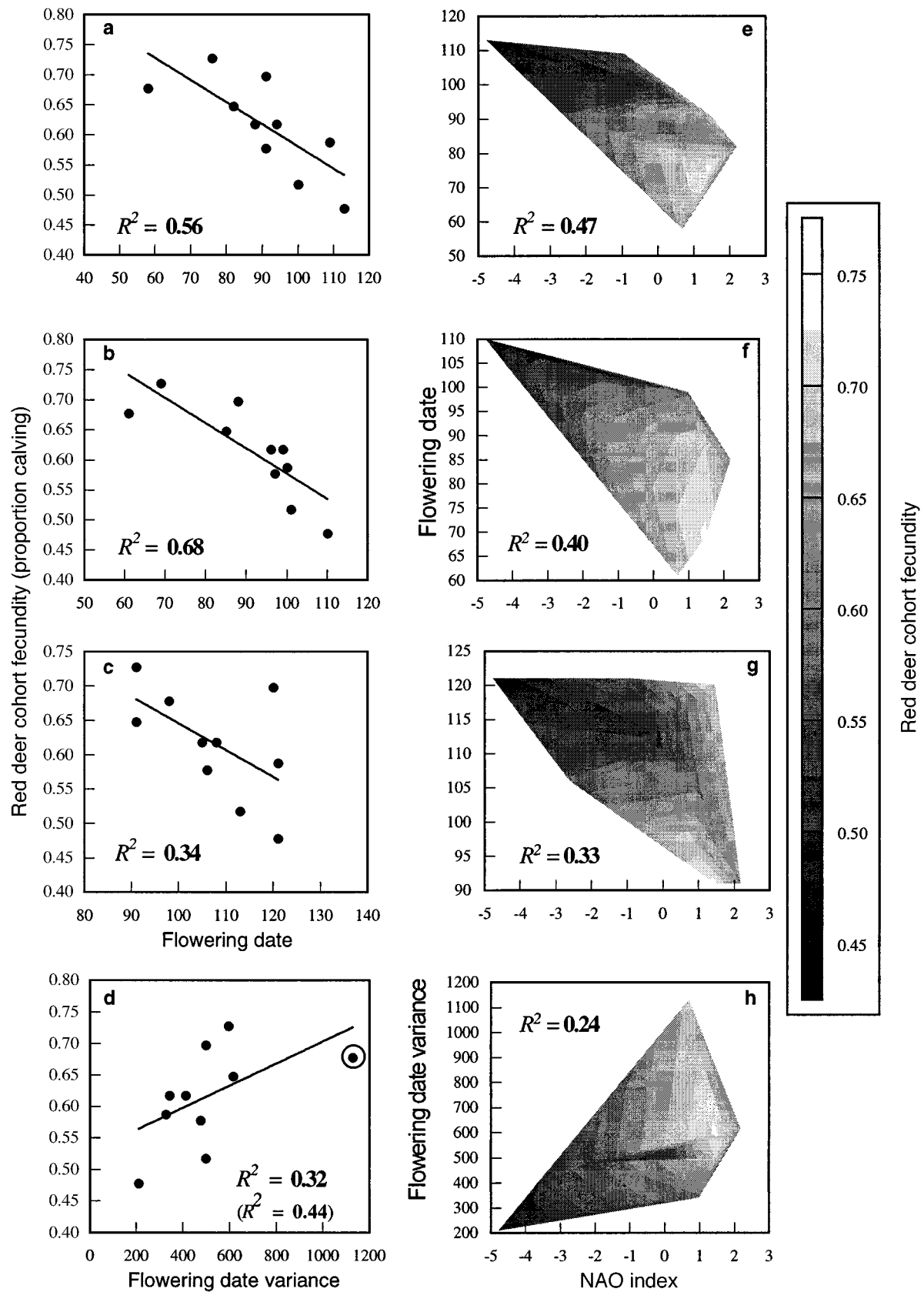
timing of flowering by *Calluna vulgaris* and *Vaccinium myrtillus* (Fig. 3), neither of which displayed much site-specific response to the NAO (Table 2). Although our analysis of the influences of large-scale climatic variability on plant phenology covered widely disparate regions of Norway, the results suggest interactions between climate and landscape that could also operate on more local scales, such as seasonal ranges of ungulates.

Climatic variability and phenotypic variation in ungulates

Variability in winter weather related to the NAO influenced the growth of moose, red deer, and Soay sheep from six populations in northern Europe. In most cases, body masses of juveniles, yearlings, and adults were influenced by climatic conditions encountered by their mothers during pregnancy, or during winters prior to their conception (Table 4). Moreover, winter conditions when female red deer from two populations were in utero influenced their future fecundity. The NAO also influenced relationships between plant phenology and fecundity of red deer in Norway (Fig. 6). Growth and fecundity of northern ungulates were thus influenced both directly and indirectly by large-scale climatic variability. In contrast to previous observations (Clutton-Brock et al. 1982, 1987, Albon et al. 1983b, 1987, Sand 1996), our analysis revealed only one instance of density-related phenotypic variation in red deer on Rum and no influence of density on the growth of Swedish moose. We attribute this contradiction to our treatment of autocorrelation in ungulate time series (sensu Post and Stenseth 1998) and to our removal of temporal trends in the data.

That growth and fecundity of northern ungulates were influenced by climate while cohorts were in utero, or years before their mothers conceived, suggests that winter weather operates on these traits through cumulative effects on the condition of females (Mech et al. 1987), and that effects of winter climate on early development can persist into adulthood (Post et al. 1997). Directly, wintertime thermoregulatory and locomotory costs to pregnant ungulates affect the allocation of energy and nutrients to the fetus (Clutton-Brock and Albon 1983, Mech et al. 1987, Hobbs 1989), and red deer born after snowy winters can be 10–20% smaller as adults than those born after cold, dry winters (Post et al. 1997). This type of density-independent variation in phenotypes can, if persistent, contribute substantially to population fluctuations in ungulates (Sæther 1997), and should be considered one of the main mechanisms through which large-scale climatic variability can influence the dynamics of northern ungulates.

However, interactions between climate and early development of ungulates are not straightforward. For example, growth and fecundity of red deer varied with the NAO in opposite fashion on Rum and in Norway. Warm, wet winters produced smaller, more fecund fe-



male red deer in Norway and larger, less fecund female red deer on Rum (Table 5). These results contradict documented relationships between body mass and fecundity of female red deer (Albon et al. 1983b, Langvatn et al. 1996), but this dichotomy can be understood by considering differences in wintertime climatic severity between maritime and continental regions. Winters in mainland Norway are snowy, and snow depth influences the foraging energetics of pregnant ungulates more so than does temperature (Hobbs 1989). Snowy winters, however, also precede early and spatially variable plant phenology in the following spring (Fig. 3), prolonging the availability of nutrient-rich forage (sensu Merrill and Boyce 1991), which probably promotes gains in body condition during spring and summer and contributes later to increased reproductive success (Post and Klein 1999). This explains, we propose, why female red deer born following snowy winters in Norway were more fecund than those born following cold, dry winters, even though they were smaller as adults.

On Rum and Hirta, however, the mild maritime climate results in a different scenario of plant and ungulate responses to warmer winters. Warm winters on Rum are neither snowy nor energetically expensive (Clutton-Brock and Albon 1982), and are favorable for growth of red deer in utero (Albon et al. 1987, Albon and Clutton-Brock 1988). Female red deer born on Rum after such winters are, however, faced with a warm spring during which forage quality peaks and declines rapidly (Langvatn et al. 1996). Moreover, mortality of red deer on Rum and Soay sheep on Hirta is lower during warm winters than during cold, energetically expensive winters (Boyd and Jewell 1974, Clutton-Brock and Albon 1982, Albon and Clutton-Brock 1988), which exacerbates density dependence in spring and results in poor gains in condition. Hence, as adults, red deer born on Rum following warm winters are larger (because growth in utero was good), but less fecund (because postnatal gains were poor).

Demographic responses of ungulates to climatic variability

With two exceptions (red deer in Norway and female red deer on Rum), all populations of northern ungulates declined after warm winters (Table 5). Although the increase in red deer in Norway may reflect greater fecundity of yearlings, which calved as 2-yr-olds (Langvatn et al. 1996), born following warm winters (Fig. 6), the 2-yr delayed positive influence of the NAO on female abundance on Rum is likely to be a result of greater survival of female yearlings born following warm winters in that population (Table 5).

In mainland regions, declines in abundance of ungulates probably resulted from increased costs of movement and foraging in deep snow (Watson 1971, Mech et al. 1987, Hobbs 1989) and to vulnerability to predation (Nelson and Mech 1986, Post and Stenseth 1998). The 2-yr and 3-yr lags in responses of moose and white-tailed deer in North America to warm winters (Table 5) support earlier contentions that reductions in physical condition during energetically expensive winters are cumulative and depress fecundity, survival, and recruitment in subsequent years (Mech et al. 1987). In contrast, declines in abundance in maritime regions (which are typically snow-free during warm winters) may have been due to density-dependent effects on survival (Clutton-Brock and Albon 1982, Clutton-Brock et al. 1985, 1987, 1991). For example, survival of yearling red deer on Rum increased after warm winters, and both populations of Soay sheep exhibited strong negative effects of density dependence as well as density independence during warm NAO winters (Table 5). Also, in Soay sheep, competition for resources during warm winters when density is high leads to poor fetal growth and low lamb birth mass and survival in the next year (Clutton-Brock et al. 1992). Although this effect of density on lamb mass and survival was shown previously to have no influence on the dynamics of Soay sheep (Clutton-Brock et al. 1992), interrelations between the NAO, lamb body mass, and abundance documented here (Tables 4 and 5) suggest

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FIG. 6. Scatter plots, regression lines, and three-dimensional surface plots depicting relationships between the fecundity of cohorts of red deer in Norway and the timing of flowering by plants, as influenced by the North Atlantic Oscillation (NAO) during the winter preceding the birth of red deer cohorts (1968–1977). Relationships are shown for plant species occurring in the range of the northernmost population of red deer in Norway, near Trondheim: (a) *Tussilago farfara*, (b) *Anemone hepatica*, and (c) *A. nemorosa*. R^2 values in a–c refer to relationships between the proportion of the red deer cohort producing calves as 2-yr-olds (the age of first reproduction) and annual dates of first flowering by each species. The R^2 value in (d) refers to the relationship between the proportion of the red deer cohort born that year that produced calves at the age of first reproduction two years later and the annual variance in timing of flowering across eight sites; the value in parentheses refers to the relationship when the influential point (circled) is excluded. Three-dimensional surface plots enclose all points in the regressions between plant phenology and the NAO index. R^2 values in e–h refer to relationships between plant phenology and the NAO during cohort birth years 1968–1977, whereas the spectrum of gray shades depicts the correlation between plant phenology and red deer fecundity. Thus, positive NAO winters, which were warm and snowy, were associated with early blooming and more spatially variable blooming, both of which were correlated with increased fecundity of red deer females. All regressions are significant ($P \leq 0.05$).

that fluctuations in the NAO may, in fact, contribute to the cyclicity displayed by Soay sheep on Hirta.

Notably, we observed no relationship between the NAO and winter mortality of red deer calves on Rum, the key factor limiting abundance in that population (Clutton-Brock et al. 1985). However, calf survival in red deer is closely related to birth mass (Albon et al. 1987), which was, in our analysis, unrelated to density but positively related to warm NAO winters. This suggests that warm winters on Rum can, directly through calf birth mass and indirectly through survival, exacerbate density dependence in subsequent years. Furthermore, on Rum, warm winters that promote survival of yearling red deer (Clutton-Brock and Albon 1982, Clutton-Brock et al. 1985) (Table 5) lead to increased competition for resources in the following summer, exacerbating density-dependent feedback on survival in the next winter. Consequently, abundance of males may decline in the following year, through either increased mortality (Table 5) or increased emigration (Clutton-Brock et al. 1982). This mechanism explains, we propose, why Clutton-Brock and Albon (1982) reported that winter mortality of red deer on Rum was related negatively to current winter temperatures, whereas we documented that it related positively to the NAO index (and thus winter temperatures) of the previous year (Table 5).

Conclusion

Although studies of the effects of local climatic variability have been important in revealing the influences of weather on plant phenology and the growth, reproduction, and demography of ungulates, this analysis illustrates that large-scale climatic variability can also influence these aspects of the ecology of plants and animals. Moreover, the dynamics of feral goats, Soay sheep, moose, muskoxen, and white-tailed deer were all influenced by the concerted effects of the NAO and density dependence, as was the case for red deer in Norway (Forchhammer et al. 1998a). Even though phenotypic and demographic traits of most of the 16 populations of ungulates studied in this paper had been previously reported to vary with local weather conditions, in 10 of 19 ungulate time series, the NAO explained as much or more of the variation than did local weather. We suggest that future studies of the effects of climatic change on ecosystem structure and function should continue to consider the potentially important influences of large-scale phenomena such as the North Atlantic Oscillation.

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