Population dynamics of Norwegian red deer: density-dependence and climatic variation

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We present a model on plant–deer–climate interactions developed for improving our understanding of the temporal dynamics of deer abundance and, in particular, how intrinsic (density-dependent) and extrinsic (plants, climate) factors influence these dynamics. The model was tested statistically by analysing the dynamics of five Norwegian red deer populations between 1964 and 1993. Direct and delayed density-dependence significantly influenced the development of the populations: delayed density-dependence primarily operated through female density, whereas direct density-dependence acted through both female and male densities. Furthermore, population dynamics of Norwegian red deer were significantly affected by climate (as measured by the global weather phenomenon, the North Atlantic Oscillation: NAO). Warm, snowy winters (high NAO) were associated with decreased deer abundance, whereas the delayed (two-year) effect of warm, snowy winters had a positive effect on deer abundance. Our analyses are argued to have profound implications for the general understanding of climate change and terrestrial ecosystem functioning.

Keywords: climate; density-dependence; density-independence; North Atlantic Oscillation; population dynamics; red deer

1. INTRODUCTION

The concept of population dynamics can, basically, be explored through variations in the four-dimensional *BIDE*-parameter space, including birth rates (*B*), immigration rates (*I*), death rates (*D*) and emigration rates (*E*) (Krebs 1972; Pulliam 1988), all of which are influenced by a great number of causal intrinsic and extrinsic interactions that determine the developmental process of populations (for example, Sibly & Smith 1985; Cappuccino & Price 1995). Intrinsic factors embrace all interactions between individuals within a population and are density-dependent, whereas extrinsic factors among others include stochastic, density-independent factors such as climate (Royama 1992; Cappuccino & Price 1995).

Recently, longer time series on ungulates have surfaced where, in particular, the comprehensive, individual-based studies on red deer (*Cervus elaphus* Linnaeus 1758) (Clutton-Brock *et al.* 1982, 1985, 1987*a,b,c*, 1997; Albon *et al.* 1983, 1987; Albon & Clutton-Brock 1988; Coulson *et al.* 1997) have contributed considerably to our understanding of the underlying mechanisms of density-dependence and local density-independence on population dynamics of large-bodied and long-lived species. Most importantly, population studies on red deer and other ungulates have, primarily through key-factor analysis, demonstrated that density-dependent and density-independent factors, in

concert, influence mortality and fecundity (see, for example, Sinclair 1977; Houston 1982; Clutton-Brock *et al.* 1985, 1991; see also Sæther 1997). For example, calf winter mortality, the key factor influencing changes in population number of red deer on Rum, Scotland, was negatively influenced by both the number of hinds in the population as well as weather induced effects through cohort fitness (Clutton-Brock *et al.* 1985, 1987*a,b*; Albon *et al.* 1987). Density-independence has convincingly been demonstrated earlier for red deer using local weather measurements such as temperature and precipitation (for example, Albon *et al.* 1987; Albon & Clutton-Brock 1988; Clutton-Brock & Albon 1989). Recently, it has been documented that a large-scale weather phenomenon, the North Atlantic Oscillation, significantly influences life-history characteristics of several terrestrial species (Forchhammer *et al.* 1998) including the specific effects on physical growth and fecundity of red deer, both of which relate to fitness (Post *et al.* 1997).

We present, for the first time, a statistical model which simultaneously incorporates separate effects of density-dependence and climatic perturbations on a northern ungulate living in natural habitats. We demonstrate that (i) density-dependent as well as climatic factors significantly influence the red deer populations; (ii) density-dependent and climatic effects on population development vary geographically across populations; and (iii) large-scale climatic perturbations, acting through the North Atlantic Oscillation, significantly affect the average reproductive performance of the red deer populations.

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Figure 1. A model illustrating the interactions between plants, ungulates, and climate as documented by empirical studies (see text). Abundance of deer and plants are given by N_t and P_t , respectively, whereas climate is denoted by U_t . Between each model compartment, interaction coefficients with arrows are given: ϕ_{32} and ϕ_{31} denote the direct influence on the ungulates and plants, respectively; α_{12} denote the effect of spatio-temporal plant abundance on deer abundance and α_{21} vice versa, whereas α_{22} and α_{11} are the intrinsic, self-regulating effects in deer and plants, respectively. Time intervals given in brackets denote the primary time of interaction relative to t . Dashed arrows indicate that these interactions are not considered explicitly in our modelling of temporal fluctuations of ungular abundance.

2. A MODEL: INTERACTIONS BETWEEN DEER, PLANTS AND CLIMATE

Changes in ungulate abundance can be viewed as a combined result of biotic and abiotic (i.e. climatic) influences on a spatio-temporal scale. In the biotic environment, two interactions have been reported to be a main influence on ungulate abundance: (i) intrinsic, density-dependent effects (figure 1: α_{22}) have, through depressed female fecundity and juvenile survival, a negative effect on ungulate abundance (see, for example, Sauer & Boyce 1983; Clutton-Brock *et al.* 1987*a,b*; Putman *et al.* 1996 and references therein), often lagged several years in time (see, for example, Fryxell *et al.* 1991); (ii) increased spatial and temporal abundance of plants, as documented through available biomass and length of the annual growth season, have been documented to increase ungulate abundance (figure 1: α_{12}) through the effects of increased body weight and thus reproductive performance as well as decreased age at maturity (see, for example, Albon *et al.* 1983; Albon & Clutton-Brock 1988; Forchhammer 1995; Langvatn *et al.* 1996). Also, the abiotic environment of both ungulates and plants exerts a considerable effect on their respective abundances: (i) winter mortality of ungulates is negatively influenced by

climatic conditions such as temperature, rainfall and duration of snow cover, resulting in a 1-year lagged depression of abundance (figure 1: ϕ_{32}) (Clutton-Brock & Albon 1982; Mech *et al.* 1987; Albon & Clutton-Brock 1988; Owen-Smith 1990; Putman *et al.* 1996); (ii) the spatio-temporal abundance of plants is considerably affected by climatic conditions, primarily without time-lags (figure 1: ϕ_{31}), such as increased available biomass following increased amount of rainfall (Sinclair 1979; Owen-Smith 1990) and increased length of the annual growth season following increased length of snow lie (Langvatn & Albon 1986; Langvatn *et al.* 1996; Post & Stenseth 1998*a*). In particular, following snowy winters (which are also warm), plant growth begins earlier and is more spatio-temporally variable among sites, presumably because of interactions between landscape heterogeneity and snow cover. The spatio-temporal variability in timing of plant growth across sites prolongs access to emergent forage by migratory ungulates such as red deer (Post & Stenseth 1998*a*).

Hence, we can specify the following deterministic dynamics of plant–ungulate–climate interactions:

$$N_t = N_{t-1}f(N_{t-1}, P_{t-1}, U_{t-1}), \quad (1a)$$

$$P_t = P_{t-1}g(P_{t-1}, N_{t-1}, U_t) \quad (1b)$$

where N_t and P_t are ungulate and plant abundance at time t , respectively. The functions $f(\cdot)$ and $g(\cdot)$ specify the temporal effects of ungulate density, plant density, and climate (U). Given the multiplicative nature of population growth, it is biologically reasonable to consider the interactions on a log-linear scale (Bjørnstad *et al.* 1995; Stenseth *et al.* 1996). Assuming a log-linear relation, equation (1) can be written as

$$\begin{aligned} N_t &= N_{t-1}\exp(F(X_{t-1}, Y_{t-1}, U_{t-1})) \\ &= N_{t-1}\exp(a_0 + a_1X_{t-1} + a_2Y_{t-1} + c_1U_{t-1}) \end{aligned} \quad (2a)$$

$$\begin{aligned} P_t &= P_{t-1}\exp(G(X_{t-1}, Y_{t-1}, U_t)) \\ &= P_{t-1}\exp(b_0 + b_1Y_{t-1} + b_2X_{t-1} + c_2U_t) \end{aligned} \quad (2b)$$

(Royama 1992; Stenseth *et al.* 1996, 1997), where $X_t = \log_e(N_t)$, $Y_t = \log_e(P_t)$, $\log_e(f(\cdot)) = F(\cdot)$, $\log(g(\cdot)) = G(\cdot)$ and U_t the corresponding climate term. Taking $\log_e$ on both sides of equation (2), isolating Y_{t-1} in (2*a*) and inserting this in (2*b*), we obtain the following general delay-equation of ungulate population dynamics:

$$X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \beta_2X_{t-2} + \omega_1U_{t-1} + \omega_2U_{t-2} + \epsilon_t, \quad (3)$$

where ϵ_t describes stochasticity and the remaining variance not specifically incorporated in the deterministic part of our model (equation (1)). Thus, on the basis of this model derived on the basis of empirical evidence (figure 1), we hypothesize that interactions between red deer abundance and their biotic and abiotic environments will result in patterns of direct and delayed density-dependence as well as direct and delayed, climate-related, density-independence.

3. THE DATA

(a) *Red deer*

We used data on the numbers of red deer culled (i.e. harvested) annually throughout the distribution of the

Figure 2. (a) Geographical distribution of the five red deer populations in Norway (shaded areas). For each population, the temporal population pattern is depicted as X_t (yearly log_e-transformed number of culled individuals) as a function of time (years). (b) Temporal variation in the Northern Atlantic Oscillation (NAO) index in the period 1964–1993. The NAO is described in detail in the text. (c–e) The $(1+\beta_1, \beta_2)$ parameter plane for total abundance (c), female abundance (d) and male abundance (e) in the five red deer populations in Norway. The estimated AR(2) coefficients in table 1b determine the location of the populations in the parameter plane and numbers refer to the populations specified above. Parameter combinations outside the triangle lead to extinction of the population. Inside the triangle, above the parabola, population dynamics are characterized by point stability. Below the parabola, population dynamics are damped fluctuations. These will persist if pronounced stochasticity is present. Arrows superimposed on the region below the parabola indicate the increasing gradients of fluctuation length following variations in $(1+\beta_1)$ and β_2 , respectively. For a detailed description of the model see Royama (1992) and Bjørnstad *et al.* (1995).

species in Norway over a period of 30 years (1964–1993). Data have been collected by Norwegian Institute for Nature Research from local municipal Wildlife Boards throughout the range of the red deer, geographically separating the number of reported cullings into counties. The annual cull of red deer in Norway takes place from 10 September to 15 November (Langvatn *et al.* 1996). Based on the regional topography and the distributional history of red deer throughout Norway (Langvatn & Albon 1986; Langvatn 1988; Langvatn *et al.* 1996), we were able to divide the counties covering the range of red deer in Norway into five defined populations (figure 2a). Unfortunately, no independent population censuses of red deer in Norway exist in addition to the culling numbers. Comparative data from other ungulate populations, however, do strongly support the use of cullings as a population index in time-series analyses: correlation coefficients between yearly harvest and census numbers were 0.81 ($n=26$; $p<0.001$) and 0.46 ($n=26$; $p<0.02$) for reindeer (*Rangifer tarandus*) in Norway (Reimers 1995) and wapiti (*Cervus elaphus nelsoni*) in USA (Picton 1984), respectively. Because similar consensus between cullings and population counts has been reported for other ungulates (see, for example, Van Ballenberghe 1985; Sand *et al.* 1997), we are convinced that yearly cullings of red deer in Norway (figure 2a) approximate to the real population changes over time.

(b) *The North Atlantic Oscillation*

The North Atlantic Oscillation (NAO) index quantifies atmospheric large-scale fluctuations between the sub-tropical and sub-polar regions of the North Atlantic. The NAO is quantified as the annual winter (December through March) deviation from the average (1864–1993) difference in sea level pressures measured at Ponta Delgadas (the Azores) and Akureyri (Iceland) (figure 2b). The specific state of the NAO determines the speed and direction of westerlies across the North Atlantic and exerts, therefore, a considerable, overall influence on the prevailing winter weather conditions (i.e. temperature and precipitation) in the continents on both sides of the North Atlantic (Hurrell 1995). Specifically, in coastal Europe and Scandinavia, high, positive values of the NAO characterize warm, moist winters, whereas unusually cold, dry winters are quantified as low, negative NAO values. The NAO index is updated annually by the Climate Analysis Section (Colorado, USA) and is accessible at their Internet home page (<http://www.cgd.ucar.edu:80/cas/climind/>).

Below, the temporal relation between estimated red deer abundance and NAO followed the annual culling period i.e. time t is set at the median culling date; the following winters severity, expressed by NAO, is also assigned by time t , whereas the following autumn culling starts the $t+1$ time period.

4. DETECTING DENSITY-DEPENDENCE AND CLIMATIC INFLUENCE FROM THE DATA

(a) *Direct and delayed density-dependence*

Tests for density-dependence in time series differ in their sensitivity to the temporal variations in the data and can give variable results (for examples, see Holyoak 1993; Fox

& Ridsdill-Smith 1995). Because no single test is obviously superior (see, for example, Saitoh *et al.* 1997), we applied five different independent tests on the red deer time series from Norway: (i) partial correlation coefficient analysis (Sokal & Rohlf 1995); (ii) first and second order autoregressions (Royama 1992); (iii) the randomization test by Pollard *et al.* (1987); (iv) the bootstrap test by Dennis & Taper (1994); and (v) the extended randomization test by Pollard *et al.* (1987) and Saitoh *et al.* (1997). Tests 1 and 3 were done within the framework of the Gompertz (1825) and Ricker (1954) models, respectively. The tests by Pollard *et al.* (1987), Dennis & Taper (1994) and partial correlation coefficient analysis were based on 10 000 randomized sequences. All tests were done on both non-detrended and detrended data.

(b) *Estimating the effect of density-dependence and climatic perturbations*

The effect of density-dependence can be detected in the autocovariate structure of populations, whereas density-independent climate-related factors are stochastic in nature (Royama 1992; Leirs *et al.* 1997). The statistical analysis of the covariance of population growth and density can be divided into two related approaches. The Gompertz (1825) population models regress the logged population growth (R_t) on logged density (X_t), whereas the Ricker (1954) population model analyses the regression of R_t on density (N_t) directly. Our unpublished results showed no statistical difference in applying the Ricker or Gompertz models, but tended to favour the Gompertz model approach (M. C. Forchhammer *et al.*, unpublished data). Assuming a log-linear relation in abundances and stochastic climate terms (U_t), the temporal change in population abundance can, in general, be described by an autoregressive model of order d (AR(d)) with the climate-related factors as covariates (for details see Royama 1992; Børnstad *et al.* 1995):

$$X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \beta_2X_{t-2} + \dots + \beta_dX_{t-d} + \omega_1U_{t-1} + \omega_2U_{t-2} + \dots + \omega_kU_{t-k} + \epsilon_t, \quad (4)$$

where ϵ_t is random noise with zero mean and constant variance, σ^2 . To find the most parsimonious dimension of AR(d), we used the corrected Akaike information criterion (Hurvich & Tsai 1989). We considered the alternatives of d equalling 0, 1, 2 and 3, respectively, because these are the dimensions from which biological meaning can be inferred (Royama 1992; Stenseth *et al.* 1996, 1997). The effect of the climate-related covariates were considered lagged up to two time periods (i.e. $k=2$) following the predictions of our model (equation (1), figure 1) and because this time-lag has been demonstrated elsewhere to have a pronounced effect on life histories of red deer, moose, and white-tailed deer (Post & Stenseth 1998a,b). The autoregressive coefficients were estimated using the AUTOREG procedure with maximum likelihood estimation in SAS v. 6.12 for Windows (SAS Institute Inc., 1996). Because the red deer time series were non-stationary (figure 2a), we detrended them by integrating time (i.e. year) as an additional covariate in the AUTOREG procedure (SAS Institute Inc., 1990). The SAS procedure allowed us to simultaneously estimate the autoregressive structure as well as the covariates of climate and time, i.e. by using

the raw abundance data. Because of the known spatial segregation of the sexes in red deer outside the mating season (Clutton-Brock *et al.* 1987c) and the demonstration of the specific effect of female abundance on individual fecundity (Albon *et al.* 1983), we also did autoregression on the female and male abundances, separately, in the five red deer populations. For the reasons stated above, we approached the effect of climate by directly integrating the temporal effect of the NAO, i.e. setting $NAO_t = U_t$, in equation (4).

To evaluate the relative effects of density-dependence and NAO on the temporal changes in red deer abundances, we calculated the standardized regression coefficients (b' , *sensu* Sokal & Rohlf 1995) using the GLIM procedure (SYSTAT Inc., 1992) with abundance (X_t) as the dependent variables, and lagged abundances (X_{t-1} , X_{t-2}) and climate (NAO_{t-1} , NAO_{t-2}) as the independent variables.

5. RESULTS

(a) Norwegian red deer populations and density-dependence

In all tests on the detrended data, direct density-dependence was detected in population 5, whereas only autoregression also detected direct density-dependence in populations 1 and 3. In the non-detrended data, only population 2 displayed direct density-dependence (table 1a). Delayed density-dependence was in most tests detected in populations 2 and 4, both in the detrended and non-detrended series (table 1a). Results from the separate analyses on female and male abundances, respectively, showed similar patterns, when comparing results across tests (table 1a). Comparing tests across population segments (i.e. total, female and male), however, results in the female segment being closer to those from the total segment (detrended: 95%; non-detrended: 79%) than the male segment (detrended: 58%; non-detrended: 50%).

The second order autoregressive process was the most appropriate in describing the dynamics of populations 2 and 4, showing statistically significant delayed density-dependence lagged two years. In contrast, the dynamics of populations 1, 3 and 5 were best described by a first-order autoregressive model, and all three populations exhibited significant direct density-dependence (table 1b). Focusing on female abundance, the dynamics of populations 3 and 4 shifted from first order to second order autoregressive processes characterized by significant delayed density-dependence (table 1b). Finally, analysing the isolated effect of male abundance resulted in three populations (1, 3, 5) showing significant direct density-dependence, but no delayed density-dependence (table 1b).

The estimated AR coefficients (table 1b) suggested that populations 1, 2 and 4 converge by a damped cyclic process and populations 3 and 5 converge to point stability (figure 2c). Being placed to the most right below the parabola in figure 2c, populations 1, 2 and 4 are expected to show long, cyclic fluctuations. If density-dependence operates primarily through the abundance of females, we can also predict that all populations except population 5 will show damped fluctuations (figure 2d). In contrast, if density-dependence occurs mainly as a result of male

abundance, all populations except population 4 would be expected to show point stability in their developmental process (figure 2e).

(b) The influence of climatic perturbations on red deer population dynamics

All populations except population 5 in Norway were significantly influenced by climate driven by the NAO. Deer abundance in populations 2 and 3 was directly influenced by the NAO and decreased following warm, snowy winters. In contrast, the delayed (two-year) effect of warm, snowy winters had a positive effect on deer abundance in populations 1, 3 and 4. Although non-significant, the dichotomy in direct and delayed effects of the NAO was consistent throughout all populations (table 1b). A similar significant effect of the NAO was observed in the female segment of populations, whereas only one population displayed the influence of the NAO, when analysed through the male segment (table 1b).

Overall, NAO only explained 7–19% of the change in abundance of red deer in Norway as visualized through the standardized regression coefficients (table 2). Removing the effect of density-dependence, however, showed that up to 44% of the residual variation in abundance was explained by variations in the NAO (table 2).

6. DISCUSSION

As predicted by our model, the temporal dynamics of red deer populations in Norway are significantly influenced by both competitive interactions between individuals (density-dependence) and climatic perturbations (density-independence). Both processes affected population development simultaneously, directly and in a delayed manner, and the relative influences of density-dependence and climate varied spatially across populations in Norway (table 1; figure 2c–e).

Also, the general conceptual framework of our model makes it an alternative candidate to key-factor analysis. The emergence of long time-series in ungulates makes it possible to apply autoregression analyses, thereby avoiding the inherent problems of key-factor analysis (Royama 1996; Kuno 1971; Itô 1972).

(a) Effect of density-dependent factors on red deer population dynamics

As suggested by the significance of both direct and delayed density-dependence (table 1, figure 2c–e), competitive interactions between individuals within red deer populations in Norway have two different proximate causes: direct density-dependence exerts its main effect through mortality, whereas delayed density-dependence primarily works through effects on growth and fecundity patterns. In addition to evidence from other red deer populations (Clutton-Brock *et al.* 1985, 1987a,b), the causal mechanisms for direct and delayed density-dependence, respectively, have been demonstrated in several other, mainly temperate ungulates (McCullough 1979; Houston 1982; Skogland 1990; Fryxell *et al.* 1991; Clutton-Brock *et al.* 1991, 1992, 1997; Messier 1991; Jorgenson 1993). Our separate statistical analyses of female and male segments of the five Norwegian populations showed that direct, mortality-related density-

Table 1. Summary of the results from the direct and delayed density-dependent tests and autoregressive analyses of population dynamics of red deer in Norway (1963–1994)

(Population numbers refer to those defined in figure 2*a*. (*a*) Population numbers are given under the respective tests if significant ($p \leq 0.05$) density-dependence was detected. Em rules ‘—’ indicate that no populations showed significant density-dependence. All five time series were non-stationary (figure 2*a*) and tests were performed on both the detrended and the non-detrended time series. (*b*) Coefficient estimations through AR-modelling were performed on detrended time series. Sample size (n) is number of years. AIC_c is the minimum of the calculated AIC_c profile for the dimension (d) range from 0–3. The specified dimension relates to the most parsimonious dimension (i.e. at AIC_c minimum). ΔAIC_c gives (if $d \neq 2$) the difference between the profile minimum and the AIC_c for $d=2$. A $\Delta AIC_c \leq 1$ is considered to be insignificant (Sakamoto *et al.* 1986). AR(2) of ‘yes’ or ‘no’ denotes whether the AR(2) model is the most parsimonious or not.)

(*a*) Results from the direct and delayed density dependent tests

	direct density-dependence				delayed density-dependence					
	partial correlation coefficient ^a		AR (1) ^b	Pollard <i>et al.</i> ^c	Dennis & Taper ^d		partial correlation coefficient		AR(2) ^f	Pollard <i>et al.</i> ^g
	Gompertz	Ricker			Gompertz	Ricker	Gompertz	Ricker		
total population										
detrended	5	5	1,3,5	5	5	5	2,3,4	2,3,4	2,4	2,3,4
not detrended	—	—	—	2	2	2	2,4	2	2,3,4	2,4
female segment of population										
detrended	5	5	1,5	5	1,5	1,5	2,3,4	2,3,4	2,3,4	2,3,4
not detrended	1,5	5	5	2	2	2	2,4	2,3,4	2,3,4	2,4
male segment of population										
detrended	5	5	1,3,5	5	5	5	1,2	1,2	—	1,2
not detrended	1,3	—	—	2	2	2	—	—	2,4	—

^aFirst (order) partial correlation coefficient of R_t on X_t and X_{t-1} (Gompertz assumption) and R_t on N_t and N_{t-1} (Ricker assumption).
^bThe first order autoregressive model.
^cThe randomization test by Pollard *et al.* (1987) with Pearson's correlation coefficient as the test value (Saitoh *et al.* 1997).
^dThe bootstrap test by Dennis & Taper (1994) based on linear regression of R_t on X_t (Gompertz assumption) and linear regression of R_t on N_t (Ricker assumption).
^eSecond (order) partial correlation coefficient of R_t on X_t and X_{t-1} (Gompertz assumption) and R_t on N_t and N_{t-1} (Ricker assumption).
^fThe second order autoregressive model.
^gThe extended randomization model by Pollard *et al.* (1987) with the partial regression coefficient as test value (Saitoh *et al.* 1997).

(b) Estimated autoregressive and covariate coefficients from the statistical population model in equation (5)

population	<i>n</i>	<i>AIC_c</i>	<i>d</i>	ΔAIC_c	AR (2)	AR (1) ^a -coefficient (1+ β_1) ^b ±s.e.	AR (2) ^a -coefficient		NAO ^a -coefficient	
							(1+ β_1) ^b ±s.e.	β_2 ^c ±s.e.	ω_1 ^d ±s.e.	ω_2 ^d ±s.e.
<i>total population</i>										
1	30	17.13	1	1.19	no	0.560±0.178	0.718±0.214	−0.287±0.214	−0.031±0.031	0.068±0.031
2	30	−53.13	2	—	yes	0.893±0.089	1.544±0.200	−0.677±0.214	−0.021±0.006	0.003±0.006
3	30	−52.38	1	2.00	no	0.716±0.126	0.966±0.225	0.013±0.222	−0.014±0.005	0.012±0.005
4	30	−35.92	2	—	yes	0.861±0.101	1.350±0.171	−0.615±0.168	−0.002±0.009	0.017±0.008
5	30	0.78	1	1.51	no	0.631±0.162	0.545±0.214	0.135±0.231	−0.004±0.023	−0.004±0.023
<i>female segment of population</i>										
1	30	54.77	1	1.97	no	0.117±0.215	0.115±0.221	−0.034±0.225	−0.037±0.045	0.084±0.039
2	30	−41.71	2	—	yes	0.891±0.088	1.333±0.194	−0.480±0.191	−0.016±0.007	−0.004±0.007
3	30	−45.01	1	0.60	yes	0.764±0.120	0.965±0.191	−0.476±0.192	−0.018±0.007	0.001±0.009
4	30	−28.80	2	—	yes	0.879±0.097	1.492±0.157	−0.720±0.152	−0.007±0.009	0.020±0.008
5	30	24.61	1	0.99	yes	0.451±0.190	0.377±0.210	0.199±0.230	−0.030±0.035	0.002±0.036
<i>male segment of population</i>										
1	30	10.83	1	1.88	no	0.530±0.187	0.494±0.219	0.075±0.227	−0.005±0.027	0.025±0.027
2	30	−52.24	1	1.79	no	0.859±0.105	0.994±0.213	−0.095±0.218	−0.004±0.007	0.007±0.007
3	30	−46.97	1	0.26	yes	0.709±0.146	0.521±0.201	0.258±0.207	−0.014±0.006	0.015±0.006
4	30	−30.70	2	—	yes	0.784±0.124	1.013±0.203	−0.315±0.202	−0.005±0.011	0.007±0.011
5	30	−7.99	1	0.74	yes	0.636±0.151	0.493±0.210	0.214±0.227	−0.008±0.019	0.008±0.019

^aSignificant coefficients ($p < 0.05$) are given in bold.^bTwo-tailed t -test, H_0 : (1+ β_1) = 1.^cTwo-tailed t -test, H_0 : $\beta_2 = 0$.^dTwo-tailed t -test, H_0 : $\omega_k = 0$.

Table 2. *Standardized regression coefficients and correlation coefficients of NAO and abundance of red deer in Norway (1964–1993)*

(Standardized regression coefficients ($\pm$ s.e.) were obtained using GLIM (SYSTAT Inc., 1992). Pearson's least squares correlation coefficients were calculated between lagged NAO indices and the residuals (δ_i) from the pure AR models on abundance, i.e. the residuals from the AR given by equation (4) with $\omega_i=0$. Bold values indicate significance at $p < 0.05$.)

population	standardized coefficients				correlation coefficients	
	X_{t-1}	X_{t-2}	NAO_{t-1}	NAO_{t-2}	$\rho(\delta_i; NAO_{t-1})$	$\rho(\delta_i; NAO_{t-2})$
1	0.92 ± 0.07	—	-0.07 ± 0.04	0.12 ± 0.03	-0.32	0.42
2	1.44 ± 0.17	-0.48 ± 0.16	0.01 ± 0.01	0.06 ± 0.01	-0.29	0.31
3	0.97 ± 0.03	—	-0.03 ± 0.01	0.08 ± 0.01	-0.21	0.66
4	1.22 ± 0.19	-0.29 ± 0.19	0.01 ± 0.00	0.08 ± 0.07	-0.10	0.43
5	0.86 ± 0.09	—	0.02 ± 0.01	0.09 ± 0.08	0.18	0.12

dependence was observed both in females and males. In contrast, the general effect of delayed, fecundity-related density-dependence was lower in males when compared with the effect of the female segments. Delayed density-dependent responses in males were detected in populations 1 and 2, but not as consistently across tests as the patterns seen in the female segment of populations, as well as in the total populations (table 1), suggesting that the sex differences in sociality described for the Rum red deer (Clutton-Brock *et al.* 1982, 1985) also operate in Norway. In the Rum population, males disperse significantly more than females, resulting in aggregated matrilineal groups sharing home-ranges outside the breeding season, and interactions between the sexes occur mainly in the breeding season. Thus, our results suggest that for red deer in Norway, fecundity is primarily influenced by female density, whereas mortality is probably influenced by both female and male densities. Although the demonstrated two-year lagged density-dependent effects (table 1b) correspond to the observed first-age of reproduction of females in Norway (Langvatn *et al.* 1996), we cannot, on the basis of the model presented here, determine whether the documented delayed density-dependence is cohort specific or whether its effect is across adult female age-groups.

If time lag responses occur mainly through the density of females in the population, as demonstrated for red deer above, we would expect the oscillatory pattern to be especially pronounced when analysing the dynamics of the female segment (*sensu* Fryxell *et al.* 1991). In fact, this was what we observed for red deer populations in Norway, where all populations but population 5 could be characterized as fluctuating when analysed through the female segment solely (figure 2d).

(b) *Effect of climatic perturbations on red deer population dynamics*

The biological explanation for the contrasting direct and delayed effects of the NAO on red deer populations in Norway (table 1b) is found through the combination of direct abiotic influence, spatio-temporal dynamics of plant phenology and density-dependent effects. Snowy winters (high NAO) generally lead to increased over-winter mortality, resulting in decreased abundance the following year (Post & Stenseth 1998a). The delayed (two-year), positive effect of high NAO, we propose, is a result of the documented increase in fecundity of cohorts born

following snowy winters (through improved forage quality and spatio-temporally increased plant growth season) (Post *et al.* 1997; Post & Stenseth 1998a), because red deer in Norway calve for the first time at the age of two years (Langvatn *et al.* 1996). Testing the effect of NAO with a lag of three years, we only obtained a significant effect in one population (M. C. Forchhammer, unpublished data).

Our results show that the effect of climatic perturbations are, as observed for density-dependence, sex-specific and suggest that the effect of NAO primarily operates through the female segment of populations (table 1b). This dichotomy probably exists because fecundity, as compared with mortality, of red deer females in Norway is consistently more sensitive to variations in NAO (Post & Stenseth 1998a), and, as our analyses show (table 1), delayed, fecundity-related density-dependence is linked to female abundance.

The temporal dynamics of the northernmost population (population 5) were apparently only influenced significantly by density-dependent processes (table 1b), which is similar to the low effect of NAO on the spatio-temporal variations of plant phenology in northern Norway (Post & Stenseth 1998a), further corroborating the trophic interactions specified in our model (figure 1). Also, the NAO has both a delayed positive (i.e. fecundity) and a direct negative (i.e. mortality) effect of red deer population change in Norway, with the positive effect being relatively larger (table 2). This suggests that the significantly increasing trend in the NAO over the past 30 years (figure 2b; Hurrell 1995) has caused an increase in numbers of red deer seen in populations 1–4 (figure 1a), through increased fecundity of females. Furthermore, because of the close relation of the NAO to regional as well as global weather conditions (Hurrell 1995), we argue that any long-term changes in climate, like global warming, will leave, through the action of NAO, their signature on the red deer populations as well as the environment. Indeed, the Pacific counterpart of the NAO, the El Niño Southern Oscillation, disrupts through cascading effects, terrestrial ecosystems in South America, leaving its signature in the long-term fluctuations in abundance and composition of mammals and other species (see, for example, Jaksic *et al.* 1994, 1997; Brown *et al.* 1997).

On a regional basis, 30–50% of the interannual variation in winter precipitation in Norway over the past 75 years is accounted for by variations in the NAO (Hurrell 1995); taking a global perspective, fluctuations in the NAO

explain approximately 55% of interannual variation in global temperatures (Schlesinger & Ramankutty 1994). This, combined with the fact that NAO has pronounced causal effects on the ecology of red deer in Norway, both directly through abiotic conditions as well as indirectly through the quality of forage, individual fitness and population development (Post *et al.* 1997; Post & Stenseth 1998a; this study), provide us with a robust set of causal relations between climate change and life history of red deer and other northern ungulates. Only further detailed studies of the life histories and time series of northern ungulates can validate whether the NAO has a similar significant influence on all northern ungulates and terrestrial ecosystem functioning in general. Nevertheless, the results emerging from our study on the effect of NAO on red deer populations in Norway, implicate the profound significance of long-term monitoring of large-bodied species in our effort to reveal the influence of climate change in the North Atlantic region.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute towards production costs.