NONLINEAR EFFECTS OF CLIMATE AND DENSITY IN THE DYNAMICS OF A FLUCTUATING POPULATION OF REINDEER

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Abstract. Nonlinear and irregular population dynamics may arise as a result of phase dependence and coexistence of multiple attractors. Here we explore effects of climate and density in the dynamics of a highly fluctuating population of wild reindeer (*Rangifer tarandus platyrhynchus*) on Svalbard observed over a period of 29 years. Time series analyses revealed that density dependence and the effects of local climate (measured as the degree of ablation [melting] of snow during winter) on numbers were both highly nonlinear: direct negative density dependence was found when the population was growing ($R_t > 0$) and during phases of the North Atlantic Oscillation (NAO) characterized by winters with generally high (1979–1995) and low (1996–2007) indices, respectively. A growth-phase-dependent model explained the dynamics of the population best and revealed the influence of density-independent processes on numbers that a linear autoregressive model missed altogether. In particular, the abundance of reindeer was enhanced by ablation during phases of growth ($R_t > 0$), an observation that contrasts with the view that periods of mild weather in winter are normally deleterious for reindeer owing to icing of the snowpack. Analyses of vital rates corroborated the nonlinearity described in the population time series and showed that both starvation mortality in winter and fecundity were nonlinearly related to fluctuations in density and the level of ablation. The erratic pattern of growth of the population of reindeer in Adventdalen seems, therefore, to result from a combination of the effects of nonlinear density dependence, strong density-dependent mortality, and variable density independence related to ablation in winter.

Key words: *Arctic; attractors; climate; density dependence; mortality; nonlinear population dynamics; North Atlantic Oscillation (NAO); phase dependence; phase–space geometry;* Rangifer tarandus platyrhynchus; *reindeer; Svalbard.*

INTRODUCTION

Nonlinearity in population dynamics arises from the actions of multiple concurrent equilibria related primarily to the properties of stage-structured and trophic interactions (Bjørnstad and Grenfell 2001). If present, such coexisting equilibria, whether stable (i.e., attractors) or unstable (i.e., repellors), can create a variety of different realizations of the manner in which a population may develop over time. To which equilibrium the population trajectory is attracted depends on the initial settings (May 1973, Cushing et al. 1998). Shift in population dynamics caused by perturbations of vital rates, trophic interactions, and environmental condi-

tions may happen in two conceptually different ways. Short-lived perturbations in vital rates or in environmental conditions can alter the dynamics of a population by forcing it into a new region of the existing phase space, though without changing the geometry of that space (Henson et al. 1998, Bjørnstad and Grenfell 2001). In contrast with this, permanent changes in vital rates or in trophic interactions or shifts in environmental regimes may change the configuration of the phase space, resulting in a marked bifurcation as the dynamics switch from one region of it to another (Costantino et al. 1995). The dynamics of natural populations probably result from interplay between these two mechanisms.

Evidence for the existence of multiple population equilibria is found in laboratory studies in which experimental manipulation of demographic and trophic interactions has led to unpredictable shifts between stable fix points and large amplitude fluctuations,

PLATE 1. Svalbard reindeer in late winter (April). (Left) Adult female and her calf. (Right) Access to forage can be greatly restricted by snow which, although never deep on the tundra, may become icy, hard, and impenetrable. Under such conditions reindeer, like this adult female, are confined to forage in small, snow-free patches. Photo credits: N. J. C. Tyler.

respectively (McCauley et al. 1999). Changes in vital rates and, hence, in the stage structure of populations are clearly important: Costantino et al. (1995) demonstrated the manner in which variation in mortality rates alone determined whether the resultant dynamics were attracted by stable-point or two-cycle equilibria.

Notwithstanding May's (1973, 1976) observation that nonlinear dynamics can be generated in simple models that include no environmental forcing, it is evident that abiotic factors can have profound effects on the dynamics of populations, owing to either cyclic (e.g., seasonal) or random changes in state variables or population parameters. Weather conditions in winter, for instance, had a profound effect on the dynamics of the population of Soay sheep (*Ovis aries*) on St. Kilda (Coulson et al. 2001). Similarly, length of season was a major factor determining interpopulation variance in the structure of the dynamics of populations of voles (Hansen et al. 1999, Stenseth et al. 2002). Large variation or marked shifts in climatic regimes may cause population trajectories to switch between multiple attractors leading to qualitative and quantitative alterations in the resultant dynamics (Henson et al. 1998).

In this paper we examine multiple and concurrent nonlinear effects of climate and density on the dynamics of a population of Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Vrolik 1829; see Plate 1) over a period of almost three decades that spanned a significant shift in climatic regime. In common with other populations of northern ungulates that have been closely monitored for a long time (e.g., Soay sheep; Clutton-Brock and Pemberton 2004), the density of this population of reindeer fluctuates vigorously from year to year (Tyler

and Øritsland 1989), resulting in an erratic pattern of growth characteristic of nonlinear time series (Bjørnstad and Grenfell 2001). We therefore integrated the effects of density dependence and climatic variation on the population using an established conceptual modeling approach (e.g., Turchin 1995, Dennis and Otten 2000, Taper and Gogan 2002) and confronted loglinear autoregressive (AR) population models (Royama 1992) with nonlinear self-exciting threshold autoregressive (SETAR) models (Tong 1990). As a novel approach, we investigated nonlinearity in several phase dimensions concurrently.

Previous studies using SETAR models have focused on thresholds in only one dimension, related to the phase of population growth (Framstad et al. 1997, Stenseth et al. 1998*a*, Post et al. 2002) or the phase of population density (Grenfell et al. 1998, Stenseth et al. 1998*b*, Ellis and Post 2004). There is, however, no reason to assume that the dynamics of populations display phase dependence only in single dimensions. On the contrary, the presence of coexisting attractors has already been demonstrated experimentally (Cushing et al. 1998, McCauley et al. 1999). Here we analyze the long-term dynamics of a natural population of large herbivores in the High Arctic and contrast time series analyses and temporal variability of vital rates across two phases of population growth and two phases of climate.

MATERIALS AND METHODS

Study area and reindeer population

The study was undertaken in Adventdalen (Fig. 1A), a broad, glacial valley in Nordenskiöld Land, central Spitsbergen, which, together with associated side valleys,
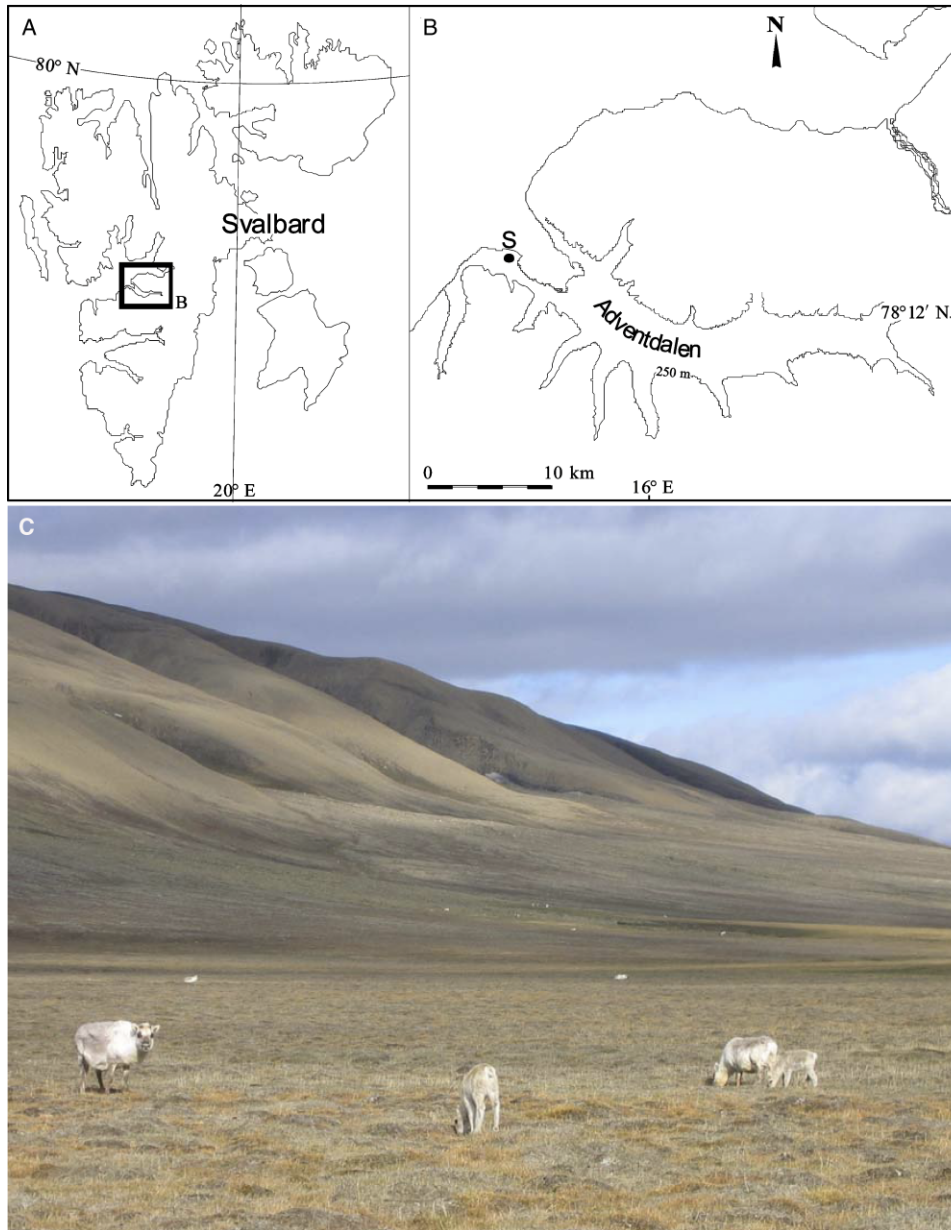
Fig. 1. (A) Map of Svalbard showing the location of the study area (box). (B) Study area delineated diagrammatically by the contour at 250 m above sea level; S marks the location of Svalbard Airport where the meteorological data were recorded. (C) Svalbard reindeer are conspicuous on the tundra in midsummer before they have molted their light winter coats, making them easy to count. This photograph, taken during the 2004 census, shows two adult females and two three-week-old calves in the foreground and a further 10 reindeer in the background.

constitutes an area of ~175 km^2 below 250 m above sea level (Fig. 1B). All reindeer in the study area were counted annually during 1979–1984 and 1988–2007 in a single census normally lasting 8–10 d and conducted in late June/early July (mean date of start of census = 29 June, SD = 8.3 d), shortly after calving, by four to six persons who walked through the area simultaneously in a sequential manner along separate, fixed, circuitous routes (Tyler 1987). The data are therefore total counts

from one nonreplicated sample each year. Most of the area is open tundra and polar semidesert, and the reindeer, which live in small groups (usually fewer than four animals), are conspicuous in midsummer before they have molted their gray and white winter coats (Fig. 1C). Moreover, they move around remarkably little within seasons (Tyler and Øritsland 1989) and the likelihood of missing or double-counting animals therefore appears only small. Consequently, the ob-
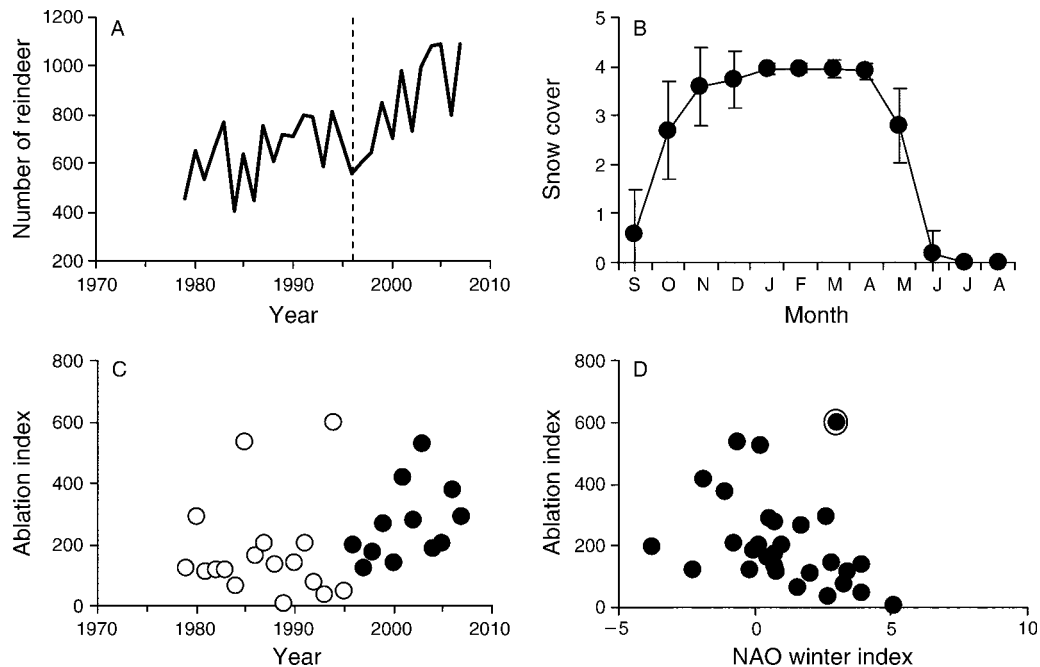
Fig. 2. (A) Time series of the annual total counts of reindeer in Adventdalen. The vertical dashed line indicates a change in climate regime. The period 1975–1995 was characterized by generally high North Atlantic Oscillation (NAO) winters while the period 1996–2007 had generally low NAO winters. (B) Snow cover at Svalbard Airport, estimated in quarters (monthly mean ± SE; data from the Norwegian Meteorological Institute 1976–1996). Snow cover was highly variable in early winter (October through December) but extensive and little variable in mid- and late winter (January through April). (C) Time series of annual ablation index (degree of snow melting) for October–December (A_{od}; see *Methods: Climate*) in Adventdalen divided with respect to phase of the NAO: open circles, high NAO (1979–1995); solid circles, low NAO (1996–2007). (D) Annual ablation index A_{od} 1979–2007 as a function of the NAO. The correlation coefficient for all years is $r = 0.34$ ($P = 0.10$); excluding the circled outlier, $r = 0.51$ ($P = 0.01$).

served large interannual fluctuations in numbers are considered real and not related to observation errors, a view supported by the fact that our analyses revealed significant nonlinearity in the relationship between population growth and population density (see Freckleton et al. 2006).

Reindeer were recognized in three age classes: calves (aged 2–4 weeks on 1 July), yearlings (aged 12–13 months), and adults (aged ≥24 months). Adults were classified by sex. Data for 1985–1987, collected using the same methods, were provided by the Norwegian Polar Institute. The combined series revealed that the population increased slowly from 1979 to 1995 but rapidly in the second part of the time series from 1996 to 2007. In addition, numbers fluctuated vigorously from year to year throughout (Fig. 2A). There are no large herbivores on Svalbard besides the reindeer, which suffer neither significant predation nor hunting (Tyler 1987).

Vital rates

Population rates of mortality and fecundity were calculated for each year. At each census in 1979–1984 and 1988–2007 the study area was searched systematically for the carcasses of reindeer that had died during the preceding 12 months. Carcasses were inspected to determine the proximal cause of death and marked to ensure that they were correctly assigned by year (Tyler

1987). Altogether 1414 of 1688 recorded deaths were attributed to natural causes, of which the majority (83.1%) were due to starvation in winter. Annual starvation mortality was defined as the number of individuals dying from starvation between 1 June year $t - 1$ and 31 May year t. The observed annual rate of starvation mortality varied between 0% and 19.3% ($n = 25$).

Reindeer are monotocous and although twinning can occur, it is exceedingly rare in Svalbard (N. J. C. Tyler, *unpublished data*). Calf production was therefore recorded from the presence of a calf (alive or dead) and where there was clear evidence of females having given birth even though no calf was observed (see Bergerud 1964, Whitten 1995). In such cases, the calves were assumed to have died and been abandoned. Other cases of perinatal mortality would have been recorded as unsuccessful calving but the error is likely to have been small owing to the low annual level of perinatal mortality in this population ($n = 0$–14 [range]; Tyler 1987; N. J. C. Tyler, *unpublished data*). Late calving would have been recorded as infertility but this error is also likely to have been small because most (>90%) calves are born in the first two weeks of June (Tyler 1987), which is before the start of the annual census. Annual fecundity, expressed as the proportion of calves per 100 females

aged ≥24 months at calving, was highly variable (mean = 55.0%; range 9.0–85.6%, $n = 29$).

Climate

Snow is a major determinant of the availability of forage on Arctic ranges in winter (e.g., LaPerriere and Lent 1977, Skogland 1978) and, because starvation in winter was the principal cause of mortality in the study population, winter weather was considered an important extrinsic factor which potentially might influence the annual scale of mortality among the reindeer.

As is typical for the High Arctic, there is little accumulation of snow in Adventdalen: the mean depth of snow at Svalbard Airport in April (deepest month) is 24.4 ± 13.1 cm (mean ± SD; data for 1977–1992 are from the Norwegian Meteorological Institute). This is considerably less than the depth through which reindeer/caribou will dig to find food in soft, friable snow (50–120 cm; Pruitt 1959, Henshaw 1968, Brown and Theberge 1990), and so we focused instead on conditions likely to influence the hardness of the snowpack (Plate 1). The successive cycles of thawing and refreezing that occur periodically during winter in the Arctic, particularly over coastal habitats, can cause the density and hardness of snow to increase to a degree at which the animals' access to the forage beneath becomes severely restricted (Vibe 1967, LaPerriere and Lent 1977, Skogland 1978, Miller et al. 1982, Adamczewski et al. 1988). The hardening of the snowpack is proportional to the degree of melting of the snow (ablation) within each period of thawing and the frequency of such thaw–freeze cycles. These two factors are integrated in the ablation index, A (sensu Forchhammer and Boertmann 1993), which quantifies heat input for the melting of snow. The weather in the west of Svalbard, summarized in data collected by the Norwegian Meteorological Institute at Svalbard Airport at the western end of the study area (Fig. 1B), is typically unstable in winter. Ambient temperature fluctuates considerably and, despite the high latitude, periods of mild weather (>0°C) lasting from a few hours to several days may occur at any time in winter. On average, 10.8 periods of mild weather occur each winter (October–April) in Adventdalen (range = 5–23 periods; 1978–2007 data). The duration of these periods is highly variable (median = 2.0, range = 1–27 d; 1978–2007 data). Ablation indices (A) were calculated for each winter (October$_{t-1}$–April$_t$, $A_{oa,t-1}$) and for two periods in each winter (October$_{t-1}$–December$_{t-1}$, $A_{od,t-1}$ and January$_t$–April$_t$, $A_{ja,t}$) selected to reflect the observed temporal pattern in mean and variance of snow cover (Fig. 2B). The three indices displayed high interannual variation (CV > 50%), illustrated for A_{od} (Fig. 2C).

The North Atlantic Oscillation (NAO), the most prominent and recurrent pattern of large-scale atmospheric circulation variability in the Northern Hemisphere, has a strong impact on local climate conditions in winter in the Arctic (Hurrell et al. 2003). Annual fluctuations in the NAO/Arctic Oscillation have been associated with the interannual variability in onset of snow, snowmelt, and the number of snow-free days observed in the Northern Hemisphere over the last three decades (Bamzai 2003). We used the NAO winter index, which displays the greatest interannual and -decadal variability (Hurrell 1995) and is the index that has been associated with the observed long-term increase in the extratropical mean temperature of the Northern Hemisphere (Hurrell 1996). The NAO winter index is defined as the annual winter (December through March) deviance from the average difference in atmospheric pressure at sea level at Lisbon (Portugal) and Stykkisholmur (Iceland) normalized relative to the period 1864–1983 (Hurrell et al. 2003). In our analyses, we used index values from the National Center for Atmospheric Research (*available online*).[10] In Adventdalen, cold and dry winters are associated with high NAO indices and vice versa. Specifically, both the mean and the variance of winter ablation indices associated with high NAO winters were low, whereas in low NAO winters these parameters were high (Fig. 2D). Hence, alterations in the state of the NAO may potentially alter the interannual pattern of ablation, which, in turn, may influence the long-term pattern of the dynamics of the reindeer in Adventdalen.

Time series modeling and statistical analyses

We approached the estimation of the simultaneous effects of density dependence and climate on the dynamics of reindeer in Adventdalen using a *d*-dimensional autoregressive [AR(d)] population model with climate as an additive covariate factor (Forchhammer et al. 1998, 2002). The corrected Akaike Information Criterion (AIC$_c$; Burnham and Anderson 1998) showed that the goodness of fit of the model was not improved for $d \geq 2$: AIC$_{cd=1} = -7.68$, AIC$_{cd\in[2;6]} \geq -5.93$ (a value of ΔAIC$_c > 1$ is considered significant; Sakamoto et al. 1986) in consequence of which, and owing to the relatively shortness of the time series, we chose instead to focus exclusively on the AR(1) Gompertz loglinear model with the effects of previous winter climate as an additive covariate (C_{t-1}):

$$X_t = \beta_0 = (1 + \beta_1)X_{t-1} + \omega_1 C_{t-1} + \varepsilon_t, \qquad (1)$$

where X_t is the ln-transformed population size in year t; β_0 represents the intrinsic rate of increase without density-dependent and climatic influences (Forchhammer and Asferg 2000); $(1 + \beta_1)$ and ω_1 are the auto- and covariate regression coefficients, respectively, and ε_t is the remaining variance not explained by the deterministic model.

The effects of a given density on the development of a population of ungulates may vary according to the phase of its growth or across contrasting climate regimes

[10] ⟨http://www.cgd.ucar.edu/cas/jhurrell/indices.html⟩

TABLE 1. Results from the nonlinear self-exciting autoregressive (SETAR) models (Eq. 2).

SETAR model	Model 1: $X_t = \beta_0 + (1 + \beta_{i,1})X_{t-1} + \omega_{i,1}A_{\text{oa},t-1}$			
	$(1 + \beta_{1,1}) \pm$ SE†	$\omega_{1,1} \pm$ SE‡	R^2_{AR}	R^2_A
A) Growth-phase-dependent				
$R_t \leq 0$ ($n = 12$)	0.9802 ± 0.4157	-0.0001 ± 0.0002	0.43	<0.01
$R_t > 0$ ($n = 16$)	**0.6344 ± 0.0826**	**0.0004 ± 0.0001**	0.45	0.40
B) NAO-phase-dependent				
High NAO (early period: 1979–1995)	**−0.4572 ± 0.3324**	0.0000 ± 0.0003	0.19	<0.01
Low NAO phase (late period: 1996–2007)	**0.0846 ± 0.3702**	0.0001 ± 0.0002	0.04	0.01

Notes: In the growth-phase-dependent SETAR (A), the threshold parameter $\tau = R_t$ and the threshold value $y = 0$ yield sample sizes (n) of 12 and 16 years for the decreasing ($R_t \leq 0$) and increasing ($R_t > 0$) phases, respectively. In the NAO-phase-dependent SETAR (B), the threshold parameter $\tau =$ year and the threshold value $y = 1995$ yield sample sizes of 17 and 12 years for the high NAO phase (NAO index, 1.71 ± 0.47 [mean $\pm$ SE]) and low NAO phase (-0.17 ± 0.54), respectively. For each of the two SETARs, three models were confronted in which the covariate variable C in Eq. 2 was substituted for the ablation indices $A_{\text{oa},t-1}$, $A_{\text{od},t-1}$, and $A_{\text{ja},t}$ (see *Materials and methods*), respectively. Regression coefficients and associated SEs were estimated through bootstrapping using the Monte Carlo resampling procedure (1000 replicates) (Venables and Ripley 1999). Significant ($P \leq 0.05$) coefficients are given in boldface type. A jackknife analysis (Crawley 2002) showed that no individual response values biased the estimates. Partial R^2 values are given for the autoregressive (R^2_{AR}) and the covariate (R^2_A) components of the models.

† H_0: $(1 + \beta_{i,1}) - 1 = 0$.
‡ H_0: $\omega_{i,1} = 0$.

(Clutton-Brock and Pemberton 2004). We therefore contrasted our loglinear AR model (Eq. 1) with a nonlinear SETAR model (Tong 1990):

$$X_t = \begin{cases} \beta_{1,0} + (1 + \beta_{1,1})X_{t-1} + \omega_{1,1}C_{t-1} + \varepsilon_{1,t} & \text{for } \tau \leq y \\ \beta_{2,0} + (1 + \beta_{2,1})X_{t-1} + \omega_{2,1}C_{t-1} + \varepsilon_{2,t} & \text{for } \tau > y, \end{cases}$$
(2)

in which the threshold τ, defined by the numerical value y, separates the population time series into two different analytical phases (1 and 2). We performed concurrent SETAR analyses related to both (1) phase dependence in population growth (henceforth termed the growth-phase-dependent model) and (2) climatic phases expressed through the NAO (henceforth termed the NAO-phase-dependent model).

In the growth-phase-dependent model, we set $\tau = R_t$ ($= X_t - X_{t-1}$) and $y = 0$ (Eq. 2), thereby dividing the reindeer population time series between increasing ($R_t > 0$) and decreasing ($R_t \leq 0$) phases of growth. For the NAO-phase-dependent model, we examined the homogeneity of the NAO winter index during the period 1979–2007 using regression tree analysis (Breiman et al. 1984, Crawley 2002). The tree analysis split the NAO series at year = 1995 (least squares fitting with minimum count allowed per node = 5 and minimum improvement in the proportion reduction in error [PRE] = 0.05; Crawley 2002), which yielded a proportional reduction in deviance of 0.45. The period 1979–1995 was characterized by generally high NAO winters (1.71 ± 0.47 [mean $\pm$ SE], $n = 17$), while in the period 1996–2007 the NAO winter index was generally low (0.17 ± 0.54, $n = 12$). In the NAO-phase-dependent model (Eq. 2), therefore, we set $\tau =$ year and $y = 1995$, thereby dividing the reindeer time series between the high (1979–1995) and the low (1996–2007) NAO phases, respectively.

The effects of ablation may vary throughout the winter (Vibe 1967, Forchhammer and Boertmann 1993). Consequently, in our AR (loglinear) and two SETAR analyses (growth and NAO phase dependence, respectively) we confronted models in which the climatic covariate C was substituted for the ablation index for three different periods of winter: $A_{\text{oa},t-1}$, $A_{\text{od},t-1}$, and $A_{\text{ja},t}$, respectively.

To investigate the extent to which changes in fecundity and mortality were responsible for the results in the AR and SETAR analyses, we constructed generalized linear models (GLM; Crawley 2002) in which annual fecundity and starvation mortality, respectively, were response variables and X_{t-1} and $A_{\text{od},t-1}$ were predictor variables. The GLM analyses were performed in triplicate using data for the entire period (1979–2003), for the two growth phases (i.e., $R_t \leq 0$ and $R_t > 0$), and for the two NAO phases (i.e., 1979–1995 and 1996–2007), respectively. All analyses were performed in S-Plus 6.1 for Windows (Insightful Corporation 2002).

RESULTS

Linear and phase-dependent autoregressive analyses

The population of reindeer in Adventdalen displayed consistent negative direct density dependence ($(1 + \beta_1) < 1$; Forchhammer et al. 1998). This was evident in the AR analyses for the entire period 1979–2007: $(1 + \beta_1) \pm$ SE = -0.15 ± 0.20, -0.05 ± 0.22, and -0.17 ± 0.20 for C in Eq. 1 set at $A_{\text{oa},t-1}$, $A_{\text{od},t-1}$, and $A_{\text{ja},t}$, respectively (partial R^2_{AR} range 0.03–0.07 in the three AR models). The SETAR models, however, revealed that density dependence was related exclusively to the phase of population growth in which $R_t > 0$ (Table 1A), indicating that density had a negative effect on abundance only in years when the population increased. In contrast with this, significant direct density depen-

TABLE 1. Extended.

Model 2: $X_t = \beta_0 + (1 + \beta_{i,1})X_{t-1} + \omega_{i,1}A_{od,t-1}$				Model 3: $X_t = \beta_0 + (1 + \beta_{i,1})X_{t-1} + \omega_{i,1}A_{ja,t}$			
$(1 + \beta_{2,1}) \pm$ SE†	$\omega_{2,1} \pm$ SE‡	R^2_{AR}	R^2_A	$(1 + \beta_{1,1}) \pm$ SE†	$\omega_{1,1} \pm$ SE‡	R^2_{AR}	R^2_A
0.8726 ± 0.4165	0.0000 ± 0.0007	0.42	<0.01	0.9434 ± 0.3848	-0.0001 ± 0.0003	0.43	<0.01
0.6825 ± 0.0920	**0.0004 ± 0.0001**	0.45	0.36	**0.6453 ± 0.1105**	0.0005 ± 0.0004	0.51	0.22
-0.5059 ± 0.3506	-0.0001 ± 0.0004	0.20	<0.01	-0.3882 ± 0.2550	0.0004 ± 0.0006	0.22	<0.01
0.1572 ± 0.3075	**0.0007 ± 0.0003**	0.01	0.20	0.3084 ± 0.3692	-0.0004 ± 0.0004	0.04	0.06

dence was evident during both the low and the high NAO phases (Table 1B), indicating that density dependence in the dynamics of the population was not specifically related to either of the two climatic regimes.

The population also responded to variation in local climate expressed in terms of winter ablation (A). The linear AR analyses showed no significant influence of climate (ω_1 in Eq. 1 not significantly different from 0, $P > 0.21$, for all three linear models) but the effects of local climate on the dynamics were, instead, found to be strongly nonlinear. In particular, the growth- and NAO-phase-dependent models showed significant effects of winter ablation only when the population was growing ($R_t > 0$; Table 1A) and during the late period (1996–2007) when winters were characterized by low NAO indices (Table 1B). In these phases, increased heat input for the melting of snow in winter (i.e., high A indices) was associated with increased abundance of reindeer in the following summer. In each case, the positive effect of the total winter (October–April) ablation, A_{oa}, was related only to the level of ablation early in early winter (October–December, A_{od}) and not to ablation in late

winter (January–April, A_{ja}; Table 1). Considerably lower AIC_c values showed that using A_{od} instead of A_{ja} significantly improved the parsimony within and across all three sets of models (the linear AR models, the nonlinear growth phase models, and the NAO phase models; Table 2).

Based on simple goodness of fit, the nonlinear growth-phase-dependent model (Fig. 3B) described the dynamics of the time series considerably better than either the NAO-phase-dependent (Fig. 3C) or the linear AR model (Fig. 3A). Moreover, two-dimensional phase space plots of the three models defined by density state variables (X_t and X_{t-1}) and fitted to the same data set showed markedly different fluctuating trajectories (Fig. 3D–F). In particular, the growth-phase-dependent model displayed large-amplitude fluctuations (Fig. 3E), while the NAO-phase-dependent model dynamics were characterized by small-scale fluctuations (Fig. 3F). The corrected Akaike Information Criterion showed that the growth-phase-dependent model with A_{oa} as an additive climatic covariate was the most parsimonious (Table 2).

TABLE 2. Model evaluation based on the corrected Akaike Information Criterion (AIC_c).

Population model	K	AIC_c	$\Delta_{i,wmo}$	$\Delta_{i,amo}$
Linear autoregressive models [AR(1)]				
Model 1 with $C_{t-1} = A_{oa,t-1}$	3	−75.70	**0.00**	6.51
Model 2 with $C_{t-1} = A_{od,t-1}$	3	−75.65	0.05	6.56
Model 3 with $C_{t-1} = A_{ja,t}$	3	−73.97	1.73	8.24
Nonlinear growth phase models [SETAR(2;2,2)]				
Model 1 with $C_{t-1} = A_{oa,t-1}$	6	−82.21	**0.00**	**0.00**
Model 2 with $C_{t-1} = A_{od,t-1}$	6	−79.40	2.81	2.81
Model 3 with $C_{t-1} = A_{ja,t}$	6	−73.38	8.91	8.91
Nonlinear NAO phase models [SETAR(2;2,2)]				
Model 1 with $C_{t-1} = A_{oa,t-1}$	6	−69.61	2.77	12.60
Model 2 with $C_{t-1} = A_{od,t-1}$	6	−76.38	**0.00**	9.83
Model 3 with $C_{t-1} = A_{ja,t}$	6	−66.43	5.95	15.78

Notes: Evaluation was performed within model types (wmo), i.e., among linear autoregressive models (ARs), growth phase self-exciting threshold autoregressive (SETAR) models, and North Atlantic Oscillations (NAO) phase SETARs, respectively, as well as across all model types (amo). Within-model type differences were related to the different periods used to calculate the ablation index, A (October–April, A_{oa}; October–December, A_{od}; and January–April, A_{ja}; see *Materials and methods*). Differences across model type were structural, i.e., AR vs. SETAR. The $AIC_c = AIC + 2K + (2K(K+1))/(n - K - 1)$, where the $AIC = n \ln(RSS/n) + 2K$, n is the sample size (29 for all models), K is the number of parameters in the model, and RSS is the residual sum of squares (Burnham and Anderson 1998). $\Delta_{i,wmo}$ and $\Delta_{i,amo}$ are the difference between the model AIC and the AIC_c value for the most parsimonious model within and across model types, respectively. The $\Delta_{i,wmo}$ and $\Delta_{i,amo}$ values in boldface type indicate the most parsimonious model.
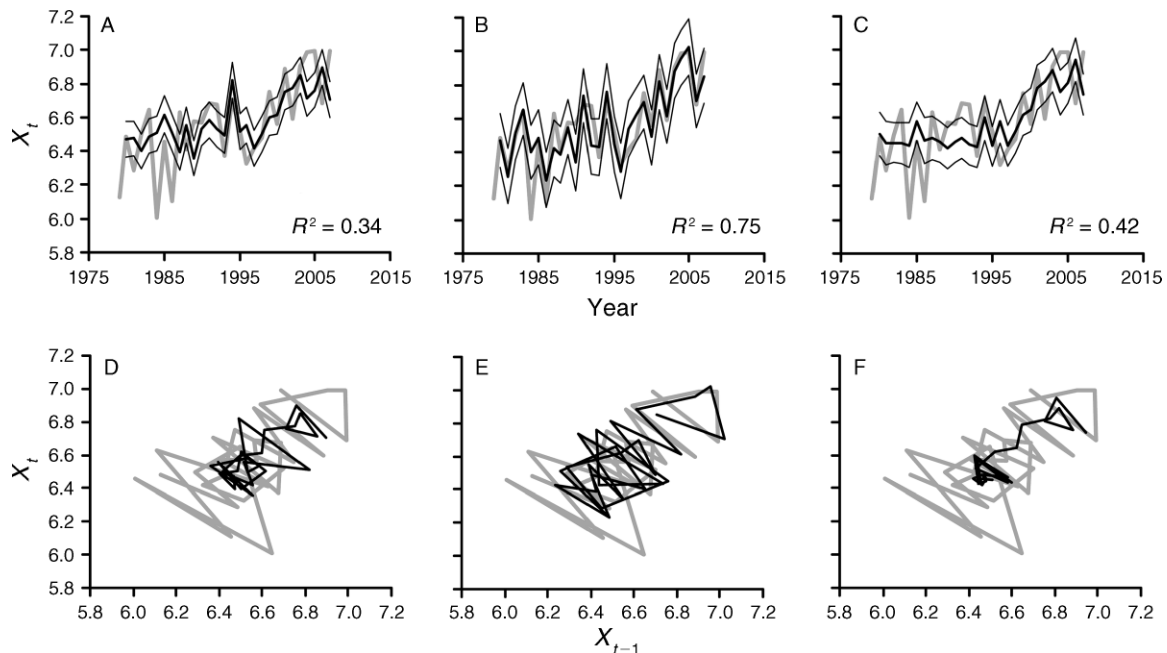
FIG. 3. Confronting models with data. Temporal dynamics of the population of reindeer (1997–2007) plotted in (A) the loglinear autoregressive (AR) model, (B) the growth-phase-dependent model, and (C) the North Atlantic Oscillation (NAO)-phase-dependent self-exciting threshold autoregressive (SETAR) model. The plots were created using the estimated auto- and covariate coefficients from Table 1 after setting the climatic covariate in Eqs. 1 and 2 at $A_{od,t-1}$. For each panel, the bold black line represents the model dynamics and the thin black lines are the bootstrapped annual SEs for each model (1000 replicates using the Monte Carlo resampling method [Venables and Ripley 1999:141]). Thick gray lines representing the actual population size (log-transformed census data, X_t) are superimposed in each panel, together with the associated R^2 values. Phase space representations are shown for (D) the loglinear AR model, (E) the growth-phase-dependent model, and (F) the NAO-phase-dependent model. The thick gray lines represent X_t.

Responses in vital rates to changes in density and climate

Annual mortality and fecundity were both density dependent but with the opposite sign: mortality increased and fecundity decreased with increasing X_{t-1}. The effect of X_{t-1} on mortality was significant across the whole period 1979–2007 (Table 3A) and in the high phase of the NAO (Table 3C) but not in either phase of population growth (Table 3B). Fecundity was density-dependent in the low (late) NAO phase only (Table 3C).

Both mortality and fecundity responded to the degree of ablation early in winter; mortality decreased and fecundity increased (Table 3) with increased ablation ($A_{od,t-1}$). The overall negative effect of ablation on mortality (Table 3A) was related to significant effects in the positive phase of population growth and in the low NAO phase (Table 3B, C). An overall association between ablation early in winter and fecundity (Table 3A) was, likewise, related to a strong positive effect during the low NAO phase (Table 3C). No association was detected between ablation and fecundity in either phase of population growth or in the high phase of the NAO (Table 3B, C).

DISCUSSION

We have demonstrated that the temporal dynamics of a food-limited, fluctuating population of reindeer are

influenced simultaneously by competitive interactions between individuals (direct density dependence) and climate perturbations (density independence). These processes had opposite effects: the growth of the population was retarded by increasing density but, contrary to expectation, was enhanced by periods of warm weather in winter (Tables 1 and 3). In a crucial manner, the relative strengths of the density-dependent and the density-independent processes that acted on the population varied with respect to the phase of its growth. The nonlinear model that incorporated this phase dependency captured a substantially greater proportion of the variance in numbers than a standard linear model (Fig. 3) and also revealed the influence of density-independent processes on the dynamics of the population that the linear analysis missed altogether (Tables 1–3). Indeed, a key aspect of our analytical approach was its focus on the pronounced nonlinearity of density-dependent and density-independent responses in the population time series (Table 1) and their associated vital rates (Table 3).

We recognize that the duration of our time series (29 years) is relatively short (but see Post and Stenseth 1999) compared with a number of recent studies that have examined the concurrent influences of density and climate on the dynamics of populations (e.g., Ellis and

TABLE 3. Results from the phase-dependent generalized linear models (GLM) with annual starvation mortality and fecundity as the response variable.

Response and predictor variables	$b_i \pm$ SE	Partial R^2	Full-model P
A. Whole-period GLM (1979–2007)			
Starvation			
X_{t-1}	**2.677 ± 0.964**	0.19	**<0.002**
$A_{\text{od},t-1}$	**−0.005 ± 0.001**	0.38	
Fecundity			
X_{t-1}	−5.486 ± 15.721	0.01	0.21
$A_{\text{od},t-1}$	**0.032 ± 0.015**	0.06	
B. Growth-phase-dependent GLM			
$R_t \leq 0$ ($n = 12$ years)			
Starvation			
X_{t-1}	−1.568 ± 2.443	0.01	0.560
$A_{\text{od},t-1}$	0.003 ± 0.003	0.08	
Fecundity			
X_{t-1}	39.130 ± 40.383	0.02	0.451
$A_{\text{od},t-1}$	−0.067 ± 0.064	0.11	
$R_t > 0$ ($n = 16$ years)			
Starvation			
X_{t-1}	1.469 ± 0.823	0.10	0.018
$A_{\text{od},t-1}$	**−0.004 ± 0.001**	0.51	
Fecundity			
X_{t-1}	21.686 ± 10.378	0.27	0.215
$A_{\text{od},t-1}$	0.008 ± 0.014	0.02	
C. NAO-phase-dependent GLM			
High NAO phase (early period: 1979–1995)			
Starvation			
X_{t-1}	**3.699 ± 1.828**	0.45	0.011
$A_{\text{od},t-1}$	−0.003 ± 0.002	0.14	
Fecundity			
X_{t-1}	−31.976 ± 26.141	0.13	0.345
$A_{\text{od},t-1}$	−0.007 ± 0.034	<0.01	
Low NAO phase (late period: 1996–2007)			
Starvation			
X_{t-1}	2.746 ± 1.569	0.16	0.05
$A_{\text{od},t-1}$	**−0.005 ± 0.002**	0.25	
Fecundity			
X_{t-1}	**−18.856 ± 10.853**	0.09	0.143
$A_{\text{od},t-1}$	**0.051 ± 0.024**	0.43	

Notes: Following the linear and nonlinear autoregressive modeling (Eqs. 1–2, Table 1), GLM analyses were performed for (A) the whole period (1979–2007), (B) the two growth phases, and (C) the two NAO phases; definitions of thresholds and sample sizes are given in Table 1. The variable b_i denotes regression coefficients (estimated through bootstrapping using the Monte Carlo resampling procedure [1000 replicates; Venables and Ripley 1999]). We also report the associated partial R-square values. Values in boldface type are significant at $P \leq 0.05$. A jackknife analysis (Crawley 2002) showed that no individual response values biased the estimates.

Post 2004). However, an analysis of similarly fluctuating dynamics in gray-sided voles, *Clethrionomys rufocanus*, found that the rate of detection of direct density dependence reached ≥97% in series lasting ≥18 years (Saitoh et al. 1998).

Nonlinear effects of density and climate

Our results suggest that the direct, negative density dependence was highly nonlinear. Specifically, density dependence in the time series of counts was related to the phase of population growth ($R_t > 0$; Table 1). When

compared, the model integrating growth phase dependence provided the single best description of the dynamics of the population (Table 2). The AIC_c model evaluation (Table 2) does not implicitly reject the possibility that the effects of climate on numbers, which were significant across the entire series, may be related to different phases of the NAO (A_{od}, Table 1) or, indeed, that the two types of phase dependency identified here may operate simultaneously as the population shifts across different phases of its growth and of the NAO (see Krebs and Berteaux 2006). Nevertheless, the current

AIC model evaluations provide little grounds for interpreting the dynamics of changes in population size beyond a single dimension.

A substantial proportion (45%, Table 3) of the increase in starvation mortality during the high (early) phase of the NAO was explained by increased density. No such density-dependent mortality was recorded in another Svalbard reindeer population (Solberg et al. 2001). However, Solberg et al. (2001) used a mortality index corrected for density in the previous year that potentially removes any density dependence in true overwinter mortality. Like Solberg et al. (2001), we found that fecundity decreased with increased population density but in Adventdalen the effect was significant only in the low NAO phase (Table 3) when the mean level of the population increased by 30% during a series of winters with high ablation (Fig. 2A, C).

The influence of local climate (variation in winter ablation, A) on the population was, likewise, nonlinear and displayed phase dependency. The SETAR models revealed significant positive effects of ablation on X_t in the $R_t > 0$ phase and the low NAO phase (Table 1). These results were supported in the generalized linear models in which significant, phase-dependent, and positive effects of ablation on both survival ($R_t > 0$ phase, partial $R^2 = 0.58$; low NAO phase, partial $R^2 = 0.50$) and fecundity (low NAO phase, partial $R^2 = 0.45$) were detected (Table 3).

The comprehensive and consistent positive effects of ablation observed here contrast with the view that mild weather in winter is deleterious for reindeer owing to icing of the snowpack, which restricts the animals' access to forage (Solberg et al. 2001, Putkonen and Roe 2003, Kohler and Aanes 2004). Hard snow and ground ice do hinder reindeer in foraging but periods of mild weather, including rain on snow, in an otherwise cold climate do not inevitably result in icing. The effects of ablation depend on how much snow is present and on what substrate it lies. Where snow is deep, surface melting may result in lower layers of the snowpack becoming saturated with water, consequently turning hard and impenetrable when subsequently they freeze. Where there is little snow and significant micro-relief, however, a similar degree of warming may result in the snowpack melting completely and the water draining away so that access to forage is actually improved rather than restricted. Consistent with this, Vibe (1967) noted that populations of caribou in West Greenland spent winter in areas where there was typically little snow and where the snowpack melted away during periods of high ablation. The animals avoided areas where snow lay deeper and did not melt away or sublime during periods of ablation (Vibe 1967). Moreover, Sámi reindeer herders evaluate the potential effect of autumn thaws ("hallemasnjacot" or "golgolnjacot") for their animals with respect to current snow cover (reindeer herder M. A. Sara, personal communication). Hence, ablation can have either positive or negative effects on the availability of forage for reindeer, depending on the amount of snow present when it occurs.

Examination of population responses to variation in local climate conditions showed that the positive effect of ablation was related statistically only to the degree of warming early in winter ($A_{od,t-1}$; Table 1). This observation reflects two aspects of the weather in Adventdalen. First, incursions of mild weather early in winter were normally substantially greater, in terms of the level of ablation, than those later in winter ($A_{od} = 211.0 \pm 28.3$; $A_{ja} = 127.1 \pm 23.1$, data 1978–2007). Second, in years in which warming had a significant effect on population growth ($R_t > 0$ phase, partial $R^2 = 0.36$, Table 1), substantial incursion of mild weather early in the season ($A_{od} = 265.7 \pm 42.6$) was frequently followed by more stable than average conditions during the latter part of winter ($A_{ja} = 118.7 \pm 18.8$). The positive effect of ablation on numbers, therefore, seems likely to have been due to the periodic occurrence of a combination of substantial melting of snow early in winter followed by colder, drier weather during the remainder of the season, both features that would have enhanced grazing conditions for the reindeer.

Our analysis of the Adventdalen time series demonstrates how even a population of a species living in a structurally simple environment, in which the vertebrate food web includes few trophic interactions (Hodkinson and Coulson 2004), can display highly complex dynamics. We have shown how the erratic pattern of growth of the population is a product of nonlinear density dependence, resulting largely from density-dependent mortality due to starvation in winter and variable density independence related to the level of ablation. Hence, under permissive conditions ($R_t > 0$), reduced levels of competitive interaction between individuals, due, in particular, to the powerful effect of incursions of mild weather in winter (A_{od}, Tables 1 and 3B), result in undercompensatory density-dependent mortality and high rates of fecundity that lead, in turn, to very rapid increases in numbers (Fig. 2A). The intermittent crashes that punctuate the time series also reflect interaction between density-dependent and density-independent forces. Though the growth phase model failed to demonstrate overcompensating density-dependent mortality, this was recorded in both the other models. The NAO phase model indicated that in the early part of the series, during which winters were characterized by a low mean level of ablation, the population was subject to strong, overcompensatory density-dependent mortality (1979–1995; Table 3C). Subsequently, conditions for the reindeer in winter became generally more favorable, though less predictable, owing to a marked increase in the level and the variance of ablation (1996–2007; Fig. 2C). The effect of density on the level of mortality was weakened during this period by the ameliorating effect of high levels of ablation (Table 3C), which in some years created conditions sufficiently favorable for the population to increase even when already at a high

density, although presumably also increasing the likelihood of a major decline as a result.

This model, in which the pattern of overcompensating density-dependent mortality largely responsible for recurrent crashes depends on the pattern across years of weather conditions in the critical season, is similar to that demonstrated by Grenfell et al. (1992) and Coulson et al. (2001) in another highly fluctuating population. Indeed, the short interval between the population crashes in Adventdalen (1–4 years; Fig. 2A) suggests that the effect of density on mortality in reindeer operates over a narrow span of population sizes at the upper end of the range, as with the sheep on St. Kilda (Grenfell et al. 1992).

Much remains to be explored. For example, the stage structure of a population can induce multiple attractors and, hence, unpredictable and qualitatively distinct dynamics (Bjørnstad and Grenfell 2001), and even small deviations in vital rates resulting from changes in population structure can produce a variety of nonlinear dynamics (Costantino et al. 1995). It may, nevertheless, be the case that highly variable and unpredictable dynamics, like those observed in the reindeer in Adventdalen, are frequently a consequence of non-linearities resulting from the existence of multiple and concurrently acting return points. Indeed, where the kind of transient and random behavior that such a situation can generate occurs independently within different populations, it may potentially counteract the synchronizing effects (Henson et al. 1998) of large-scale climate between them (Post and Forchhammer 2002, 2004).

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