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Continuous and discrete extreme climatic events affecting the dynamics of a high-arctic reindeer population

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Abstract Climate at northern latitudes are currently changing both with regard to the mean and the temporal variability at any given site, increasing the frequency of extreme events such as cold and warm spells. Here we use a conceptually new modelling approach with two different dynamic terms of the climatic effects on a Svalbard reindeer population (the Brøggerhalvøya population) which underwent an extreme icing event ("locked pastures") with 80% reduction in population size during one winter (1993/94). One term captures the continuous and linear effect depending upon the Arctic Oscillation and another the discrete (rare) "event" pro-cess. The introduction of an "event" parameter describing the discrete extreme winter resulted in a more parsimonious model. Such an approach may be useful in strongly age-structured ungulate populations, with young and very old individuals being particularly prone to mortality factors during adverse conditions (resulting in a population structure that differs before and after extreme climatic events). A simulation study demonstrates that our approach is able to properly detect the ecological effects of such extreme climate events.

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T. Severinsen Department of Biology, University of Oslo, P.O. Box 1066, Blindern, Oslo, N-0316, Norway **Keywords** Arctic oscillation · Continuous vs. discrete environmental forcing · Non-linearity · Time series analysis · Ungulates

Introduction

An improved understanding of externally driven density-independent factors has been made urgent by climatologists reckoning that we currently may be experiencing changes in both the mean and variability of the climate at any given site (IPCC 2001). The increased variability in temperature and precipitation will increase the frequency of extreme events such as cold and warm spells (Shabbar & Bonsal 2003), drought (Clark et al. 2003), wild fires (Diaz-Delgado et al. 2003) and flooding (Thomson et al. 2003) in terrestrial ecosystems and algal blooms in marine ecosystems (Chan et al. 2003b). For example, recurrent wildfires due to an increased fire frequency, as is occurring in some Mediterranean-type ecosystems (Diaz-Delgado et al. 2003), may reduce ecosystem resilience (i.e. the ability to recover the predisturbance state). Modelling the dynamic effects on ecological systems of such extreme climatic effects together with more continuous effects is thus very important, and also challenging as it relates to the issue of non-linear ecological effects of climate variability (e.g. Seastedt & Knapp 1993; Mysterud et al. 2001; Stenseth et al. 2002; Stenseth & Mysterud 2002; Mysterud et al. 2003).

In northern arctic and alpine environments, more frequent freezing and thawing are expected key features of winter climate for herbivores in the future given a global warming (Danell et al. 1999; Mysterud et al. 2003). A recent analysis showed that winter warm spells increased in both the frequency and duration over most of Canada during the second half of the 20th century, linked to more frequent occurrences of the positive phase of the North Atlantic Oscillation (NAO) (Shabbar & Bonsal 2003). Extreme icing events, typically a result of warm spells with rainfall during winter, severely restrict access to the field layer for herbivores – being termed "locked pastures" among Sami reindeer herders (Holand 2003). The "text-book" example of a dramatic effect of such locked pastures comes from the extreme northern environment on Svalbard, Norway at $78-80^{\circ}$ North. Despite that fat reserves of the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) during autumn may constitute 60% of the total body weight; a severe icing event in 1993/94 led to an 80% decline in the Brøggerhalvøya population (Aanes et al. 2002; see also Solberg et al. 2001; Aanes et al. 2000). In contrast, the effect of variability in climate apart from such extreme winters, is mainly related to differences in summer forage quality (Aanes et al. 2002).

Here we propose to model such extreme climatic events as an environmental forcing component being different from the typically assumed (linear or non-linear) response to continuous and fairly normal climate variability, namely as a component specifically corresponding to rare climatic effects (such as occasional extreme winter icing events). We have earlier adopted such an approach in another setting: Chan et al. (2003b) using the same methodological framework when analysing the population dynamical effects of an algal bloom in a marine system. Here we specifically expand on this approach within a terrestrial setting using data on the Svalbard reindeer as an example to model the potential dynamic role of the increased frequency of warm spells during winter at northern latitudes (Shabbar & Bonsal 2003). Throughout we adopt a phenomenological approach primarily aiming at determining the structure of the interaction between the biological processes and the environmental forcing due to both fairly continuous climate variability (such as the North Atlantic Oscillation and the Arctic Oscillation) and discrete extreme weather events.

Material and methods

The reindeer data

We use reindeer abundance data from the Brøggerhalvøya peninsula (221 km²) located on the north-western coast of Svalbard (78°5'N, 11°5'E); characterized by a mountainous area in the centre, surrounded by areas of lowland plain (for further details, see Aanes et al. 2000). Transferring three males and nine females to Brøggerhalvøya founded the study population in 1978. The number of reindeer has been counted annually during April from 1979 by personnel on snow-mobiles. The terrain is open and such counts are regarded highly reliable with insignificant sampling error (Aanes et al. 2000, 2002). The population grew – within the Brøggerhalvøya – steadily until a major population crash during the winter 1993/94. Data that were used derive from Øritsland and Severinsen (unpubl.; see also Aanes et al. 2000, 2002).

The climate data

Data on the North Atlantic Oscillation (NAO; Hurrell et al. 2003; http://www.cgd.ucar.edu/~jhurrell/nao.html) and the Arctic Oscillation (AO; Thompson & Wallace 1998; Stenseth et al. 2003; http://jisao.washington.edu/ data/annularmodes/Data/ao_index.html) were derived from the web. The AO and NAO are both part of the more widely defined Northern Hemisphere Annular Mode (NAM; Thompson & Wallace 2000; Thompson et al. 2000; Baldwin et al. 2003). The AO is defined as the first PC time series of the mean sea level pressure (SLP) field over the Northern Hemisphere, north of 20°N. We refer to the AO for summer (June–September) as AOs, and winter as AOw (November–April). See Stenseth et al. (2003) for pros and cons for using such indexes as opposed to local weather variables.

Additive and innovative outliers

Within a time series context, there are several notions of outliers, the distinction of which is pertinent to a proper assessment of the effects on the population dynamics due to a discrete extreme climatic event. An outlier refers to an observation that does not conform to the general (dynamical) pattern shared by the majority of the observations. This happens if, for example, the dynamics is approximately linear under "typical" conditions, but is non-linear over a wider spectrum of covariate values encompassing both typical and atypical conditions, with the single, "offending" observation outside the linear domain. Yet in a dynamic system, there are two kinds of outliers, namely, additive outlier and innovative outlier. An additive outlier occurs when the response variable takes an atypical value, which then alters the autoregressive structure for the next few time series observations. On the other hand, an innovative outlier occurs when the error term in a time series model takes an atypical value, so that the autoregressive structure is affected only for the corresponding observation. Furthermore, a dynamic system may respond to an extreme event with a level shift (i.e. the mean function changes by a certain amount afterwards). For example, this occurs if the first differences of the data (i.e., growth rates for logtransformed data) are a white noise process that has an additive outlier. Thus, the proper treatment of an extreme event in a time series analysis depends on the nature of the outlier (Tsay 1988; Peña et al. 2001).

Statistical analyses

We compared the performance of earlier models with the conceptually new model, with more details in an electronic appendix.

Let the population size in year t be given as N_t , and the corresponding log-transformed abundance as $X_t = \log(N_t)$; let furthermore $R_t = X_t - X_{t-1}$ and I_t a dummy variable indicating the winter crash of 1993/94 (being equal to 1 for t = 1994 and zero otherwise). Assuming maximally an order 2 density-dependent structure, a possible model for a lag k of the external climate (C_{t-k}) for which either the NAO or the AO (winter or summer) as well as an additional external extreme event is given as $R_t = R'_t + \delta I_t$ (where R'_t [see below] are defined as the corresponding variables had there been no crash in the winter of 1993/94). We remark that the maximal order could well be 3 because of fractional delay in the density dependence. Indeed, the reindeer were counted in April of each year and natality in reindeer in spring depends on the reindeer condition in the preceding winter which in turn correlates with abundance in the winter. Thus, if the process is affected by lag 2 of the reindeer abundance, a fractional delay of 2.5 may be expected, in which case the maximal order may become 2.5 or the maximal order becomes 3. See section 2.3.1 of Royama (1992). The issue of the maximal order will be explored empirically below.

Following in general (but not in detail) Aanes et al. (2002), we model the unperturbed R'_t as an AR model with C_{t-k} as the covariate:

$$R\prime_t = \beta_0 + \beta_1 R\prime_{t-1} + \beta_2 R\prime_{t-2} + \gamma_k C_{t-k} + \varepsilon_t, \tag{1}$$

where, as above, ε_t are uncorrelated noise terms of zero mean and constant variance, β_i and γ are coefficients and k = 0, 1, 2 is to be selected by the AIC (the Akaike Information Criterion).

Thus, we may speculate that the 1993/94 crash mainly perturbed the growth rate in 1994; that is, $R_t = R'_t + \delta I_t$. Upon substituting this relationship in (1) and after rearranging, we obtain

$$R_{t} = \beta_{0} + \beta_{1}R_{t-1} + \beta_{2}R_{t-2} + \gamma_{k}C_{t-k} + \delta I_{t} - \beta_{1}\delta I_{t-1} - \beta_{2}\delta I_{t-2} + \varepsilon_{t}.$$
(2)

The 1994 reindeer datum is then modelled as an additive outlier, referring to the perturbation being localized in the particular growth rate in 1994. Model (2) implies that the observed growth rates were affected for 3 years starting from 1994. The model is essentially comparing the natural mean level before (16 years) and after (5 years) the icing event, after adjusting for the natural growth rate and serial dependence. Note that a 5-year post-intervention period is not atypical for such studies (Ramirez & Crano 2003).

In contrast to modelling the 1994 crash as an additive outlier, an alternative is to consider the crash effect as an innovative outlier (i.e., its effect is localized in the residual in 1994), so that the model becomes

$$R_t = \beta_0 + \beta_1 R_{t-1} + \beta_2 R_{t-2} + \gamma_k C_{t-k} + \delta I_t + \varepsilon_t.$$
(3)

Under this scenario, the unperturbed model may be estimated by omitting the single outlying data case.

While the use of dummy variables to model atypical events is not new, the different ways of placement of the dummy variables as in (2) and (3) correspond to different types of outliers, namely, innovative and additive outliers each with different implications on the model dynamics (for definition of these two types of outliers, see above). This distinction of various outlier types, while well known in time series literature, seems to have received little attention in the ecological literature.

Results

All models reported below were fitted using a modified ARIMA function of the statistical package R (http:// www.r-project.org/). It should be emphasized that the original ARIMA function in R and the ARIMA procedure of SAS, as well as the SPSS trends package do not fit models such as (3). Rather, they model the covariate-adjusted variable as an ARIMA model (i.e., $m_t = \beta_0 + \beta_1 m_{t-1} + \beta_2 m_{t-2} + \varepsilon_t$ where $m_t = R_t - (\gamma_k C_{t-k} + \delta I_t))$ (i.e., fitting a regression model with the errors specified as an ARIMA process). This subtle difference in the model estimated by the major statistical software from the intended biological model may for sure easily be overlooked!

The Brøggerhalvøya populations had significant direct and delayed density dependence (see also Aanes et al. 2000, 2002). The first row of Table 1 reports the model defined by (2) fitted to all data, with the lag of the AOs as the covariate in the best-fitted model selected by the AIC. As predicted, dropping the crash effect from the best fitted model results in worse fit, i.e. higher AIC (second row in Table 2), and further omitting the 1994 datum also leads to a worse fit (c.f. third row in Table 2). The top panel of Fig. 1 shows that the fitted values from the best fitted model match the observations closely. The predicted values for the years 2000-4 appear to extend the trend of the data smoothly. The middle panel of Fig. 1 shows that omitting the crash effect renders the fitted model to grossly over-predict the number of reindeers in 1994 but otherwise tracking the data reasonably well. However, the predicted values appear to be depressed when compared with the data trend, possibly due to the smaller estimates of the intercept and the AOs effect (in magnitude), when compared with the first model. But dropping the 1994 datum from the model fit still yields a substantial over-prediction of the 1995 datum, as seen in the bottom panel of Fig. 1. Also, the predicted values seem to be at a lower level than suggested by the data.

Model (2) implies that the reindeer data follow an order 3 process.

To empirically check whether order 2 suffices for the original process, we fitted a model modified from (2) with R_{t-i} replaced by X_{t-i} i=1,2, but the AIC of the modified model is -9.63, well above that of the order 2 model for the growth rates. Hence, we conclude that an order 2 model for the growth rates is consistent with the observed data. Note that (2) can be re-written as $R_t = \beta_0 + \beta_1 X_{t-1} + (-\beta_1 + \beta_2) X_{t-2} - \beta_2 X_{t-3} + \gamma_k C_{t-k}$

Model Eq. 2 (in $\mathbf{R}_t = \mathbf{X}_{t-} \mathbf{X}_{t-1}$)	Intercept	Density dependen	се	Climate-continuous	Climate-event	Error	AIC
	β_0	β_1	β_2	γ	δ	Q_7	
Full model	0.4465 (0.0644)	-0.5316 (0.1588)	-0.4190(0.1481)	AOs _{r-2} -0.2941 (0.0809)	-1.9021 (0.0973)	0.01168	-19.69
$\mathbf{R}_{t} = \beta_{0} + \beta_{1} \mathbf{R}_{t-1} + \beta_{2} \mathbf{R}_{t-2} + \gamma_{2} \mathbf{AOS}_{t-2} + \varepsilon_{t} \text{ (all years, without encode affract})$	0.1296 (0.1034)	-0.1084 (0.2269)	0.0761 (0.2370)	AOs _{t-2} -0.0762 (0.3662)		0.1745	31.87
$\mathbf{R}_{t} = \beta_{0} + \beta_{1} \mathbf{R}_{t-1} + \beta_{2} \mathbf{R}_{t-2} + \gamma_{2} \mathbf{AOS}_{t-2} + \varepsilon_{t} \text{ (excluding 1994, without crash effect)}$	0.0761 (0.0663)	0.5284 (0.2194)	-0.2225 (0.2160)	AOs _{t-2} 0.1372 (0.2244)		0.07053	15.22

+ $\delta I_t - \beta_1 \delta I_{t-1} - \beta_2 \delta I_{t-2} + \varepsilon_t$. Substituting the estimates from the first row of Table 1 in the preceding equation, we see that the coefficient estimates of lags 1–3 of X_t and their standard errors (enclosed in parentheses) equal -0.532 (0.16), 0.0216 (0.16) and 0.419 (0.15) respectively. Thus, it seems that the aforementioned lag 2.5 effect is better picked up by the lag 3 proxy than the lag 2 abundance. Moreover, this shows clearly that the process is density dependent.

According to model (2), the population exhibits a crash effect due to the severe winter 1993/94, and the dynamic was altered for 3 years starting from 1994 but then recovered afterwards. By dynamic, we mean the autoregressive structure of the model for the observed growth rates. Figure 2 displays the time plot of the residuals from the fitted model specified by model (2), as well as the residual autocorrelations, which indicates that the residuals appear to be white. As climate may interact with the density dependence structure (Stenseth et al. 2004; Jacobson et al. 2004; Ciannelli et al. 2004), we have tested for possible interactions between climatic effects and lagged growth rates using the test of Chan et al. (2003a). Specifically, we consider a nonparametric version of (2) by letting the density-dependent effects and the climatic effect to be possibly nonlinear, i.e. $R_t = \beta_0 + s_1(R_{t-1}) + s_2(R_{t-2}) + s_3(C_{t-k}) + \delta I_t - \beta_1 \delta I_{t-1} - \beta_2 \delta I_{t-2} + \varepsilon_t$, an additive model where s_i are nonparametric functions to be estimated from the data. We then test whether the model contains significant interaction terms as products of pairs of the nonparametric main effects, namely, $s_1(R_{t-1})$ $s_2(R_{t-2})$, $s_1(R_{t-1}) s_3(C_{t-k}), s_2(R_{t-2}), s_3(C_{t-k})$, one by one, using the method of Chan et al. (2003a).

We outline the testing procedure for checking the significance of, e.g. $s_1(R_{t-1})s_2(R_{t-2})$ as follows: Let the residuals from the original model be e_t . Fit an additive model similar to the original additive model but with the response variable now being $s_1(R_{t-1})s_2(R_{t-2})$. Let the residuals of the latter additive model be f_t . The test statistic is $T = nR^2/(1-R^2)$, where *n* is the sample size, R^2 is the *R*-square from the linear regression of e_t on f_t . The test statistic has a χ^2 asymptotic distribution with 1 d.f., under the null hypothesis that the model is additive, i.e. the interaction term is absent from the model. The *p*-values of the three interaction terms equal 0.16, 0.76 and 0.1, suggesting that the system is additive. Moreover, the additive effects are found to be by and large linear, with the d.f. of s_1 , s_2 and s_3 estimated to be 1.31, 1 and 1 respectively. Altogether, these model diagnostics suggest that the growth rates can be adequately modelled by a single auto-correlation model specified by model (2), even though theoretically the growth rate may be initially non-stationary given its somewhat small founding population (see Royama 1992: 112–113).

The coefficient estimates are all insignificant for lags 0–2 of AOw and NAO, and for lags 0 and 1 of AOs. The last two models in Table 1 correspond to the two general AR models fitted by Aanes et al. (2002), see corrected results in Aanes et al. (2004).

of post-intervention data. The table reports the percentage of rejecting the null hypothesis of no climatic effect (i.e., the null hypothesis that $\delta = 0$, at 5% significance level). Each experiment had 1000 replications of simulated time series. Percentages in the column under the heading $\delta = 0.0$ are the empirical size of the test, all of which are close to the nominal 5% value

No. of post-intevention data	$\delta = 0.0$	$\delta = -0.1$	$\delta = -0.5$	$\delta = -1.0$	$\delta = -1.5$	$\delta = -2.0$
2	8.7	18.7	99.4	100	100	100
5	6.6	16.2	99.5	100	100	100
10	7.0	22.6	99.2	100	100	100

We have also explored the possibility of modelling the crash effect as an innovative outlier, but the AIC of the best-fitted model equals -12.16 [relative to the model defined by Eq. (2)], suggesting that the additive outlier specification [i.e., the model given by Eq. (2) with AIC = -19.96] is the better. Therefore, we conclude that the 1993/94 crash is adequately modelled as an additive outlier.

Fig. 1 Solid curve displays the logarithm of the reindeer counts in Brøggerhalvøya, with crosses for the fitted values from three models (Table 1). The fitted values and the predicted values displayed in the top graph are computed from the model defined by Eq. (2) fitted with all data. Those in the middle graph are from the model defined by (2) without the crash effect, again fitted with all data whereas the fitted values in the bottom graph are from the model defined by (2) without the crash effect and fitted with all data except the 1994 datum



Fig. 2 The upper diagram shows the time plot of the residuals for the fitted model specified by Eq. (2). The lower diagram is the corresponding residual autocorrelation function. The dotted horizontal lines are the 95% confidence limits assuming the errors are white noise. In particular, none of the residual autocorrelations are significant, at 5% significance level



Assessing the appropriateness of the model through simulations

We performed a simulation study specifically designed to investigate the empirical performance of the proposed approach for detecting a discrete, extreme climatic effect. Specifically we examine the effect of the length of the post-intervention period and the signal-tonoise δ/σ ratio on the size of testing for an extreme climatic effect. Abundance data of 21 years (over the same years we have the reindeer data) were simulated from a model similar to the fitted full model in Table 1. We varied the number of post-intervention data as 2, 5 or 10. Table 2 reports the empirical percentages of rejecting the null hypothesis of no climatic effects using a nominal 5% *t*-test derived from the estimator of δ . It can be seen that the empirical level of the test is generally close to 5% although somewhat inflated to 8.7% when there are only two post-intervention data. The test has moderate power if the climatic effect is of the same order of magnitude as the noise standard deviation, but its empirical power becomes almost 100% when the δ/σ ratio approaches 5. Overall, the empirical power curves for different post-intervention number of data bear similar shape, as is expected from general statistical theory. While the dominating factor for detecting an extreme climatic effect is the δ/σ ratio, Table 2 shows that in the case of an extreme climatic effect occurring very close to an end of the time series, it may be desirable to do an adjustment to account for size inflation of the t-test (e.g., by bootstrap). In our case, such an adjustment is not needed as the empirical level is quite close to the nominal 5%. Indeed, the bootstrap 95% confidence interval of the crash effect parameter (δ) extends from -2.09 to -1.68 (based on 1000 bootstraps with the residuals sampled with replacement), which almost equals the theoretical interval from -2.11 to -1.70, thereby strongly indicating the significance of the found crash effect.

Discussion

Our approach is of potential great use when studying the ecological effects of climate – with occasional extreme events. For example, discrete shocks may be detected by testing the significance of the coefficient of the dummy variable for an (additive or innovative) outlier sequentially case by case, with proper allowance for the multiple tests, see Tsay (1988) and Peña et al. (2001). Alternatively, the outliers may be modelled through an approach of probabilistic mixture of two normal distributions, one of which having a much larger variance accommodates occasional extreme events, see p. 143 of Peña et al. (2001).

Our approach may be particularly useful for studying strongly age-structured populations (see, e.g., Gaillard et al. 1998) whose population structure may differ before and after rare and extreme climatic events. For ungulates, survival of prime-aged females is typically stable and high, but lower and more variable among both young and old individuals (review in Gaillard et al. 1998). Importantly, density-dependent and densityindependent variation in vital rates interacts strongly with the age structure in determining the dynamics (Coulson et al. 2001). When conditions are severe, either due to high density, harsh climate, or the interaction, young and old individuals are most strongly affected constituting the bulk of the dying individuals (Coulson et al. 2001, for Svalbard reindeer, see Solberg et al. 2001). The introduction of a "climate-event" parameter in addition to a continuous climate variable is a way of incorporating a sudden change in sex and age structure after a population crash. The 1993/94 crash resulted from heavy climate-induced emigration and some mortality (Øritsland and Severinsen unpubl). Younger individuals are also the ones most frequently dispersing (Wahlström & Liberg 1995; Clutton-Brock et al. 2002), so also increased emigration can lead to a different population age structure. Irrespective of the demographic mechanisms, Eq. (2) indicates that the crash triggered a 3-year alteration in the dynamics starting from 1994 even after accounting for the sudden drop in density (table 1), demonstrating the utility of such an approach for ungulate populations. It should be mentioned that our approach is not limited to time series analysis of population counts; it might, given data, easily be lifted to an age-structured analysis that may pinpoint the differential impacts of the extreme events on different age group; see Chan et al. (2003b) for a related application. Unfortunately, age-structured data are unavailable for the reindeer population under study.

The probability of a severe die-off (> 50% decline in total population size in one year) is 14% per generation in vertebrates (Reed et al. 2003). Observing that extreme climatic events may imprint signatures on the ecological dynamics, it might be worthwhile analysing what the emergent properties in a wider geographical context are, for instance, in relation to the ability of such extreme events to provoke population-size oscillations and to synchronize different populations exposed to the same extreme events. However, this is beyond the scope of this particular paper. Another issue concerns finding some climatic factor that correlates well with the crash. While this problem is of general interest, such a task may be futile here given only one major crash in the reindeer data. Indeed, any such climatic factor must have an extreme value in 1994, but otherwise within normal range. The dummy variable which equals 1 in 1994 and 0 otherwise forms the ideal limit of any such climatic factor. Thus, for the purpose of untangling the normal weather impact from the extreme but rare weather impact, our approach is perhaps the best one could have.

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