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Modelling non-additive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example

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Understanding how climate can interact with other factors in determining patterns of species abundance is a persistent challenge in ecology. Recent research has suggested that the dynamics exhibited by some populations may be a non-additive function of climate, with climate affecting population growth more strongly at high density than at low density. However, we lack methodologies to adequately explain patterns in population growth generated as a result of interactions between intrinsic factors and extrinsic climatic variation in non-linear systems. We present a novel method (the Functional Coefficient Threshold Auto-Regressive (FCTAR) method) that can identify interacting influences of climate and density on population dynamics from time-series data. We demonstrate its use on count data on the size of the Soay sheep population, which is known to exhibit dynamics generated by nonlinear and non-additive interactions between density and climate, living on Hirta in the St Kilda archipelago. The FCTAR method suggests that climate fluctuations can drive the Soay sheep population between different dynamical regimes—from stable population size through limit cycles and non-periodic fluctuations.

Keywords: Soay sheep (*Ovis aries*); density dependence; population cycles; climate effects; time-series analysis

1. INTRODUCTION

Given the potential ecological effects of climate change, a current major challenge is to characterize the dynamic effects of extrinsic climate fluctuation (Stenseth *et al.* 2002; Walther *et al.* 2002). This is not a trivial task, as climate can interact with other factors, such as population density (Coulson *et al.* 2001), degree of interspecific competition (Sætre *et al.* 1999), grazing impact (Mysterud *et al.* 2003) and human harvesting (Stenseth *et al.* 2002), in determining species distribution and abundances. Although the relative importance of intrinsic factors and extrinsic environmental variation in determining the dynamics of animal populations has long been a central theme in population ecology (Nicholson 1933; Andrewartha & Birch 1954; Turchin 1995; Leirs *et al.* 1997; Grenfell *et al.* 1998; Berryman 1999; Coulson *et al.* 2001; Lima 2001), the interactive effects of climate and population density have usually been ignored (but see Coulson *et al.* 2001). Interactions between climate and other factors may yield complex dynamics that are not appropriately modelled using linear systems.

Following May's pioneering work (May 1974), the degree to which populations are limited by nonlinear intrinsic processes has been explored in detail (Royama 1977, 1992; Berryman 1978, 1981, 1999; Sugihara 1994; Falck *et al.* 1995; Stenseth *et al.* 1998*a*; Turchin & Ellner 2000). Ricker (1954) focused on the dynamic effects of nonlinearity before May (1974); however, it was May's writing that made this topic a focal one among ecologists. Later, the possibility of such nonlinearity in the effect of extrinsic factors was also recognized (Jewell *et al.* 1974; Grenfell *et al.* 1992, 1998; Mysterud *et al.* 2001). However, few methodologies allow disentangling of the effects of intrinsic factors and extrinsic climatic variation in situations in which, for example, the climatic effect is stronger at high than at low population densities. Such interacting effects can be seen in a few simple systems following detailed longitudinal individual-based demographic measurements (Coulson *et al.* 2001). However, such detailed and long-term data are extremely rare. Most long-term datasets from monitoring are time-series of total counts, and we need a method for identifying patterns that are likely to be caused by nonlinear and non-additive effects from such data.

Using the long-term data of annual counts of Soay sheep (*Ovis aries*) from Hirta in the St Kilda archipelago (figure 1*a*,*b*), we demonstrate, in a time-series setting, a

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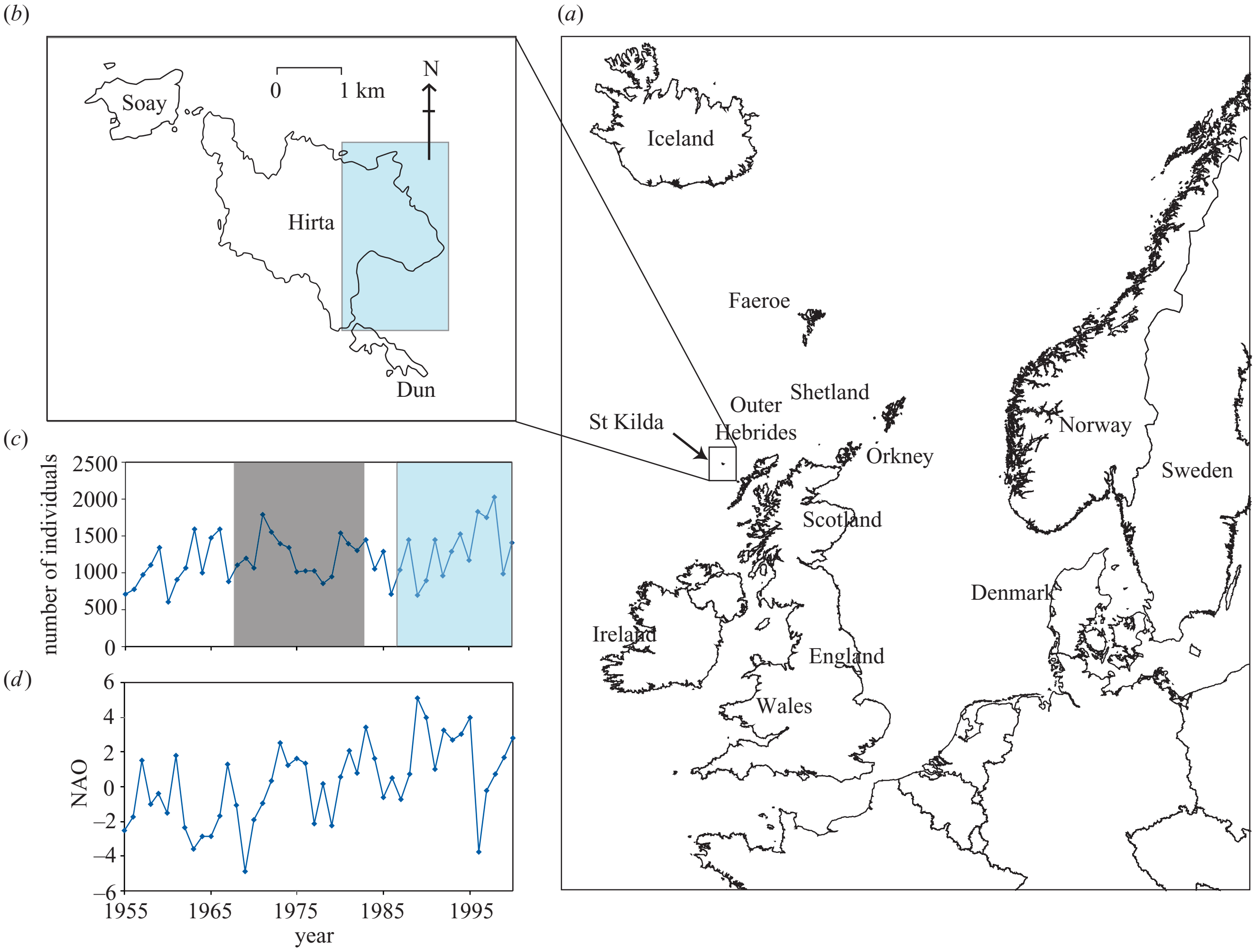

Figure 1. The study site, Hirta (*b*) in the St Kilda archipelago off the coast of Scotland (*a*). The Soay sheep count data are given in (*c*) and the NAO index for the corresponding years are given in (*d*). The blue-shaded area in (*b*) represents the Village Bay catchment—the area within which the individual-based studies were carried out—these data are used to develop the ASSM model (see § 3a). The quality of the count data within the grey-shaded segment of (*c*) is unknown. However, the climatic effects detected by the new time-series method seem to be robust to slight measurement errors. We assessed the effects of measurement errors with a simulation study by adding normal errors with zero mean and standard deviation equal to one-tenth of the observed standard deviation over the period from 1970 to 1984 to the log-sheep counts. For each of the 50 replications, we repeated the estimation procedure described in § 3a, and all fitted models of the 50 replications chose 2 d.f. for the B(NAO) spline function, as is the case for the original logarithmic sheep counts.

pattern that is consistent with the hypothesis that extrinsic climate fluctuations affect the intrinsically generated direct density dependence in a nonlinear and non-additive manner. The proposed approach allows the simultaneous identification of nonlinear density dependence and non-additive effects of extrinsic factors (e.g. Chan *et al.* 2003) even when the extrinsic effects on the population dynamics are also nonlinear (Jewell *et al.* 1974; Grenfell *et al.* 1992, 1998; Mysterud *et al.* 2001). As such, our paper has a double focus, helping to characterize the dynamics of the Soay sheep as well as providing a methodological contribution to the analysis of time-series data in order to infer how intrinsic and extrinsic processes might determine the dynamic structure of the population, and how this may affect the dynamics of the growth rate.

2. THE SOAY SHEEP POPULATION

The data on the dynamics of the Soay sheep population on Hirta consist of detailed individual-based data on marked animals that have been collected in the Village Bay catchment of the island since 1985 (figure 1*b*). In addition, there have been annual estimates of the total island population size since 1955; these are the data used in this study. Several approaches have been used to model both of these datasets (Grenfell *et al.* 1992, 1998; Catchpole *et al.* 2000; Coulson *et al.* 2001; Forchhammer *et al.* 2001). The current understanding is that the dynamics of the Soay sheep result from a complex interaction between population density, winter weather, and the age and sex structures of the population (Coulson *et al.* 2001). The Age-Structured Markov Model (ASMM) reported by Coulson *et al.* (2001) describes the dynamics well and provides accurate predictions of future population sizes given the correct weather inputs. The model is complex, with 32 parameters, and contains functions describing density-dependent and density-independent sex- and age-specific survival and fecundity functions (see electronic Appendix

A for a discussion of the fit to the data as compared with our threshold autoregressive (TAR) model).

Most ecological data do not consist of sufficiently detailed records to warrant such a complex modelling approach. Indeed, most long-term data consist of counts. This begs the question of how much of the underlying biology can be accurately inferred from analyses of such counts. We develop a method for inferring a process previously undetectable with existing time-series methods—a method that may enable us to extract important information about the ecology–climate interaction for a broad variety of systems for which only count time-series are available.

3. THE DATA

(a) *Sheep data*

Feral sheep populations on islands of the St Kilda archipelago, UK, have been monitored since 1955 (Jewell *et al.* 1974; Grenfell *et al.* 1992, 1998; figure 1*c*). There is some ambiguity concerning the quality of counts between 1968 and 1984. Our simulations demonstrate that our results are not an artefact of the ambiguity of this segment of the data (see legend to figure 1*c*).

(b) *Climate data (the North Atlantic Oscillation)*

The North Atlantic Oscillation (NAO; Hurrell 1995; Hurrell *et al.* 2003; see also Stenseth *et al.* 2003) is a large-scale fluctuation in atmospheric mass between the subtropical North Atlantic region (centred on the Azores) and the sub-polar North Atlantic region (centred on Iceland) (Lamb & Peppler 1987). As an index for the global winter climate, we used Hurrell's winter NAO index (Hurrell 1995), which is based on the difference of normalized sea level pressures between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland for December–March (http://www.cgd.ucar.edu/~jhurrell/nao.html#winter). The NAO is positively related to winter rainfall on the west coast of Scotland (Hurrell 1995; Catchpole *et al.* 2000) and has been shown to affect fecundity and survival in Soay sheep (Milner *et al.* 1999; Catchpole *et al.* 2000; Forchhammer *et al.* 2001). The NAO has been detrended by fitting a natural cubic spline with 5 d.f. (see § 4 (equation (4.4)) for further discussion on the natural cubic splines). We have focused on detrended NAO values in order to avoid trends in the NAO leading us to find spurious effects owing to the trend itself (as opposed to the fluctuation in the NAO, which is, after all, the key focus of this climate index). We have also repeated the analysis below (see § 5) with the raw NAO, with similar conclusions.

4. INCORPORATING CLIMATE EFFECTS ON THE STRENGTH OF THE DENSITY DEPENDENCE IN POPULATION MODELS

Simulation with the ASMM has predicted that the degree of over-compensatory density dependence might vary as a function of the underlying climate (Coulson *et al.* 2001). Indeed, even in the case of the Soay sheep, we do not have data for a sufficient number of years to test this prediction, yet the time-series of island counts may (when analysed by the method proposed in this paper) be long enough to detect short-term dynamical phases in the structure of the dynamics that result from climate fluctuations. In order to model the count data, we use the basic model adopted by Grenfell *et al.* (1992) and Moorcroft *et al.* (1996):

$$N_t = N_{t-1}\left(R_0\Big/\left[1+(N_{t-1}/K)^b\right]\right)\eta_t, \qquad (4.1)$$

where N_t is the density in year t (referred to as the counts in the summer of year t), η_t is a multiplicative noise-term, R_0 is the maximum net population growth rate, K is a parameter closely related to the carrying capacity (given as $N_e = K(R_0 - 1)^{1/b}$), and b is a parameter expressing the degree of density dependence (or the degree of overcompensation; the larger it is, the stronger the degree of density dependence or overcompensation). The dynamic properties of the skeleton of this model (i.e. $\eta_t \equiv 1$) are well understood (May 1975; Bellows 1981; see also Begon *et al.* 1996) and vary from stable population size for low R_0 and b, through regular cyclic dynamics to chaos for large values of R_0 and b.

The model given by equation (4.1) may be approximated by the continuous TAR model (Chan & Tsay 1998; Stenseth & Chan 1998). Writing $n_t = \log(N_t)$, $r_0 = \log(R_0)$ and $k = \log(K)$, equation (4.1) becomes

$$n_t = n_{t-1} + r_0 - \log(1+\exp((n_{t-1}-k)b)). \qquad (4.2)$$

For large values of b, $\log(1+\exp[(n_t - 1 - k)b])$ approximates to zero if $n_{t-1} - k \ll 0$, and to $(n_{t-1} - k)b$ if $n_{t-1} - k \gg 0$. Incorporating these approximations into equation (4.1) produces a continuous TAR model. Including a stochastic process noise component ($\varepsilon_{i,t}$ are independently and identically randomly distributed (iid) variables of zero mean, and variance σ_i^2), the model is given as

$$x_t = \begin{cases} a_0 + a_1(x_{t-1} - k) + \varepsilon_{1,t} & \text{if } x_{t-1} \leqslant k \\ a_0 + a_2(x_{t-1} - k) + \varepsilon_{2,t} & \text{if } x_{t-1} > k \end{cases}, \qquad (4.3)$$

where $x_t = \log(N_t)$, $\log(\eta_t) = \varepsilon_{1,t}$, if $x_{t-1} \leqslant k$, otherwise $\log(\eta_t) = \varepsilon_{2,t}$; $a_0 = \log(R_0) + a_1 k$, $a_1 = 1$, $a_2 = a_1 - b$, and $k = \log(K)$. Grenfell *et al.* (1998) used a similar model; however, their self-exciting threshold auto-regressive (SETAR) model (Tong 1990) was discontinuous. This model involves, at most, only six parameters.

The TAR model has several advantages over other nonlinear models such as the one defined by equation (4.2). For example, Stenseth *et al.* (1998*a*,*b*) applied the TAR models to the Norwegian lemming data and the Canadian lynx data, and the two regimes were found to correspond to the increase and the decrease phases of the highly fluctuating populations; hence the threshold model is capable of modelling density dependence and phase dependence in ecological processes. More importantly, the piecewise linearity of the TAR model simplifies the analysis of the ecological features local to a particular phase—the nonlinear perturbations when climate affects the system only in a particular phase of the process (see Royama 1992, p. 40). Statistical inferential procedures are simpler for TAR models than for the model given by equation (4.1) particularly when we extend the model to account for parametric variation in terms of climate covariates. A distinct feature of the continuous TAR model is that it is essentially a linear model, given the threshold. This makes it much easier to include climatic effects non-parametrically in the model. By contrast, the theta logistic model (Gilpin & Ayala 1973; see also Lande *et al.* 2003) and other similar nonlinear models become exceedingly complex upon non-parametrically incorporating climatic effects.

Observing that there was a non-homogenous structure of the noise-term, Grenfell *et al.* (1998) applied a somewhat similar TAR approach. We extend this approach by further modelling this noise term. We do this by testing for whether a climate proxy (the NAO) has an additive or non-additive effect on the dynamics structure; observing that the external climatic forcing has a non-additive effect, we thus develop a method for estimating this non-additive effect.

Coulson *et al.* (2001) suggested that the degree of over-compensation followed a humped distribution with an increasing NAO index—over-compensatory density dependence was greatest for intermediate mean values of the NAO, implying that b may be described as a function of the NAO (i.e. $b = \mathrm{B}(\mathrm{NAO}_t)$). We substantiate this claim through a general and generic time-series approach—an extension of the continuous TAR model (e.g. Stenseth & Chan 1998) which we will refer to as the Functional Coefficient Threshold Auto-Regressive (FCTAR) model that specifies some coefficients of the TAR model (here b) to be functions of some covariates. Because the functional form of $b = \mathrm{B}(\mathrm{NAO}_t)$ is unknown, we will model this as a spline. Specifically, in equation (4.3), we model b as a function of the NAO, and hence a_2 as a function of the NAO (i.e. $a_2 = a_1 - b(\mathrm{NAO}_t)$). We take a_2 as a natural cubic spline (i.e. a cubic spline which is linear for extreme values). The degrees of freedom (d.f.) of the natural cubic spline equal the number of coefficients specifying the piecewise cubic polynomial; in general terms, the d.f. measures the curvature of the function. For any given d.f., the natural cubic splines are conveniently parameterized in terms of the B-spline (Eubank 1999). The B-spline basis functions are computed using the ns function of the spline package of *R* (http://lib.stat.cmu.edu/R/CRAN/). For 1 d.f., the splines become constants; for 2 d.f., they are straight lines. If the d.f. $= m > 2$, the natural cubic spline $a_2(\mathrm{NAO})$ can be expressed as the sum of some scalar multiples of particular types of smoothly pasted piecewise cubic polynomials (i.e. parameterized as a linear combination of m natural B-spline bases):

$$a_2(\mathrm{NAO}_t) = \Sigma_{1 \leqslant i \leqslant m} \gamma_j N_i(\mathrm{NAO}_t). \qquad (4.4)$$

The models reported in table 1 are fitted by minimizing the AIC $= -2 \times$ (log likelihood) $+ 2 \times$ (number of parameters), calculated under the assumption of normally distributed noise in equation (4.3).

For the constrained TAR model (i.e. with $a_1 = 1$), we have $K = \exp(k)$ and $R_0 = \exp(a_0 - a_1 k)$. Assuming that $a_1 = 1$, $a_0 > 0$, $a_2 < 1$, then the equilibrium equals $\exp[(a_0 - a_2 k)/(1 - a_2)]$.

5. RESULTS AND DISCUSSION

Table 1 provides the parameter estimates for models including the NAO as a climatic covariate (Burnham & Anderson 1998). As expected, a_1 of the unconstrained model (given by equation (4.3)) is close to 1 (implying no density dependence in the lower regime). We consequently fit the constrained TAR model assuming $a_1 = 1$ (table 1*b*). All of the constrained TAR models estimate K as 1006 (s.d. $= 94.5$) and R_0 as 1.269 (s.d. $= 0.127$); the corresponding equilibrium densities will, without the NAO, be *ca.* 1241 (s.d. $= 59.2$). The appropriateness of the model is further supported by the observation that observed litter sizes are *ca.* 1.2 (Forchhammer *et al.* 2001) and that, on average, 68% of the population are females, juvenile survival over their first year is *ca.* 0.6 (Forchhammer *et al.* 2001) and yearly survival of adults is *ca.* 0.8 (Catchpole *et al.* 2000), which altogether suggest a comparable value for R_0 (*ca.* $1.2 \times 0.68 \times 0.6 + 0.8 = 1.29$).

It should be noted that the most competitive model varies depending on the assessment of fit—adjusted R^2s suggest that $b(\mathrm{NAO})$ should have 4 d.f. (a nonlinear function), whereas AICs suggest it should have 2 d.f. (a linear function; see figure 2). The adjusted R^2s are (as is typically the case in ecological time-series modelling) all relatively small. However, for the constrained model, $b()$ being a linear function of NAO explains *ca.* 8% of the residual variation of the model without NAO (i.e. a constant b function).

One probable reason for the small R^2 values is that the total sheep counts include proportions of animals in different life stages that vary independently of current population size, and that the demographic rates of these different life stages respond to climatic variation in contrasting ways (Coulson *et al.* 2001). Total count data do not capture this complexity. Consequently the effects of climate will be diluted in analyses of such data. Nonetheless, incorporating the NAO into the model almost doubles the R^2, suggesting that the observed climatic effect is profound. In electronic Appendix A, we provide a discussion of the advantages of using adjusted R^2 and AIC as measures of fit. Which model should then be considered the most appropriate? Figure 2 suggests that increasing the degrees of freedom from two to four adds a 'kink' to the shape of the function. The general impression from each of these plots suggests that the B function increases as the NAO index increases. Given the similarities between the shape of the functions with 2, 3 and 4 d.f., we consider the B function to have 2 d.f., as is suggested by AIC. Indeed, figure 2 explains why Grenfell *et al.* (1998) found the upper flat segment of their SETAR model: their model represents a compromise fit to the varying NAO values. We note that the climatic effects detected by the new time-series method seem to be robust to measurement errors; see the legend of figure 1.

The overall best model admits a rich spectrum of dynamical behaviour across a variety of NAO values. The TAR skeleton admits a globally stable limit point that decreases with increasing NAO value within the observed NAO range, but limit cycles (Chan & Tong 2001) and non-periodic behaviour emerge when NAO is extrapolated to higher values.

The long-term qualitative behaviour of the skeleton may be altered when the system is subject to dynamic process noise as specified by equation (4.3); see for example, Stenseth *et al.* (1998*a*). For example, the skeleton defined by equation (4.2) generally admits a stable limit point when the NAO is fixed at any value within the observed range of the NAO. Simulation studies (see electronic Appendix A) suggest that this qualitative behaviour seems, for all but very high NAO values, unchanged by including dynamical noise in the system. Because the decadal signal of the NAO is generally weak (Stephenson *et al.* 2000), the NAO may be viewed as an almost noise-like oscillator that further reinforces the interaction of the dynamic noise and the nonlinear skeleton, resulting in enhanced cyclicity in the process with high NAO values.

Table 1. Results from the fitting of the unconstrained and constrained continuous TAR model, with a_2 modeled as a natural cubic spline with d.f. = 1, 2, 3, 4.
(The threshold parameter, *k*, is searched from the 30th to the 70th percentiles of the data. Values of γ are the estimated coefficients of the B-spline bases, the linear combination of which is a spline function estimator of a_2. The B(NAO) = $a_1 - a_2$(NAO) can be estimated by substituting a_1 and $a_2()$ with their corresponding estimators. When the d.f. = 1, $\gamma_1 \equiv a_2$, which does not hold for d.f. > 1. Models with the lowest AIC or highest adjusted (adj.) R^2 are given in bold. Models with 1 d.f. do not have the NAO incorpora-ted as a covariate (only as a constant), whereas the models with d.f. values of between 2 and 4 do incorporate the NAO as a covariate. Standard errors of estimates are given in parentheses.)

d.f.	a_0	a_1	γ_1	γ_2	γ_3	γ_4	k	σ_1^2	σ_2^2	adj. R^2 (%)	AIC
(*a*) unconstrained model fits											
1	7.127	0.7967	−0.06434				6.914	0.01986	0.0864	4.4	−122.8
	(0.0769)	(0.218)	(0.258)				(0.121)				
2	7.132	0.8138	0.2399	−0.9721			6.914	0.01952	0.07906	9.8	**−123.8**
	(0.0890)	(0.218)	(0.508)	(0.722)			(0.135)				
3	7.125	0.7925	−0.8860	0.8971	−1.196		6.914	0.01995	0.07789	8.5	−121.9
	(0.0874)	(0.217)	(1.14)	(1.05)	(0.802)		(0.129)				
4	7.108	0.7644	−1.107	−0.6040	1.903	−2.278	6.904	0.01985	0.07102	**11.8**	−121.6
	(0.0829)	(0.229)	(1.07)	(0.609)	(1.31)	(1.49)	(0.124)				
(*b*) a_1 constrained at a fixed value of 1											
1	7.148	1	−0.1173				6.914	0.01958	0.08728	6.0	−124.7
	(0.0747)		(0.260)				(0.0817)				
2	7.152	1	0.1458	−0.986			6.914	0.01926	0.07975	11.4	**−125.7**
	(0.0852)		(0.517)	(0.660)			(0.0939)				
3	7.148	1	−0.8691	0.7394	−1.204		6.914	0.01963	0.0787	10.1	−123.8
	(0.0855)		(0.9944)	(0.972)	(0.703)		(0.0928)				
4	7.138	1	−1.171	−0.6608	1.770	−2.357	6.914	0.02068	0.07343	**12.9**	−123.3
	(0.0825)		(0.839)	(0.531)	(0.864)	(1.15)	(0.0868)				

A critical question is whether the modelling of count data can detect the climatic effects that operate in the population through age structure and other mechanistic links. We have explored this issue empirically using simulations (see electronic Appendix A).

We simulated 50 time-series of the total island population size from an ASMM (see electronic Appendix A). Each series covers 50 years. In the ASMM, survival and fecundity parameters depend on the NAO as well as previous population size and their interaction. For each simulated series, the NAO values are generated as a continuous sub-sequence of historical standardized NAO indices (i.e. (NAO − 1.73)/10 with a random starting point between 1864 and 1951). The age structure of the first time-point was identical for all series. For each simulated series, we fitted a FCTAR model with the coefficient of the lower regime constrained to be 1 and that of the upper regime being a natural cubic spline function of the detrended NAO, with d.f. ranging from 1 to 4. The d.f. required were then estimated by minimizing the AIC. The continuous TAR model detects the NAO effect in 100% of such ASMM-simulated cases; d.f. is chosen to be 2, 3 and 4 with frequencies of 7, 8 and 35, respectively.

The NAO inputs to the ASMM were then simulated as iid normally distributed variables of zero mean and standard deviation $c \times 0.2$ (roughly that of the observed centred NAO), c being proportional to the dispersion of the NAO inputs and hence the strength of the NAO effect in the simulated model. The empirical performance of the FCTAR method is summarized in table 2*a*. The c parameter was varied from 1 to 0 in the simulation study. The FCTAR method performed well. When $c \geqslant 0.25$, a NAO effect was detected on 100% of occasions (out of 1000 replicates). The FCTAR method performed less well when the NAO input was weaker; when there was no NAO input ($c = 0$) the FCTAR model correctly specified 1 d.f. on 62.4% of occasions, and when $c = 0.01$ (a weak NAO input) the method correctly specified 1 d.f. on 42.9% of occasions. Furthermore, table 2*a* suggests that the magnitude of the simulated NAO correlates positively with the d.f. chosen, revealing the nonlinear character of the climatic effect in the ASMM.

We then simulated times-series from the FCTAR model fitted to the Soay sheep data, with d.f. equal to 1 or 2 (see table 2*b*). Again, the NAO values are simulated as iid normally distributed variables with mean and standard deviations equal to −0.102 and 2.01, respectively (the observed values of their counterparts of the detrended NAO over the study period); the noises of the two regimes are assumed to be normally distributed, with the first sheep count equal to the observed count in 1955. When the true d.f. = 2, the method has a very high capability of detecting the NAO effect, which indeed is expected because the data are now simulated from a FCTAR model with a NAO effect. We note that when the true d.f. = 1, the false-positive rate decreases with increasing sample size, but is now much lower than that of the ASMM with the NAO effect suppressed. The slight disparity of these results may be because the statistical properties of the ASMM predictions and the whole island time-series differ. These differences may be attributed to the atypical five years of decline from 1973 to 1978. It is also possible that two population crashes were missed (see Besbeas *et al.* 2002).

In sum, the time-series method seems reliably to detect climatic effects in the Soay sheep system being studied in this paper. Recent research has demonstrated that a wide

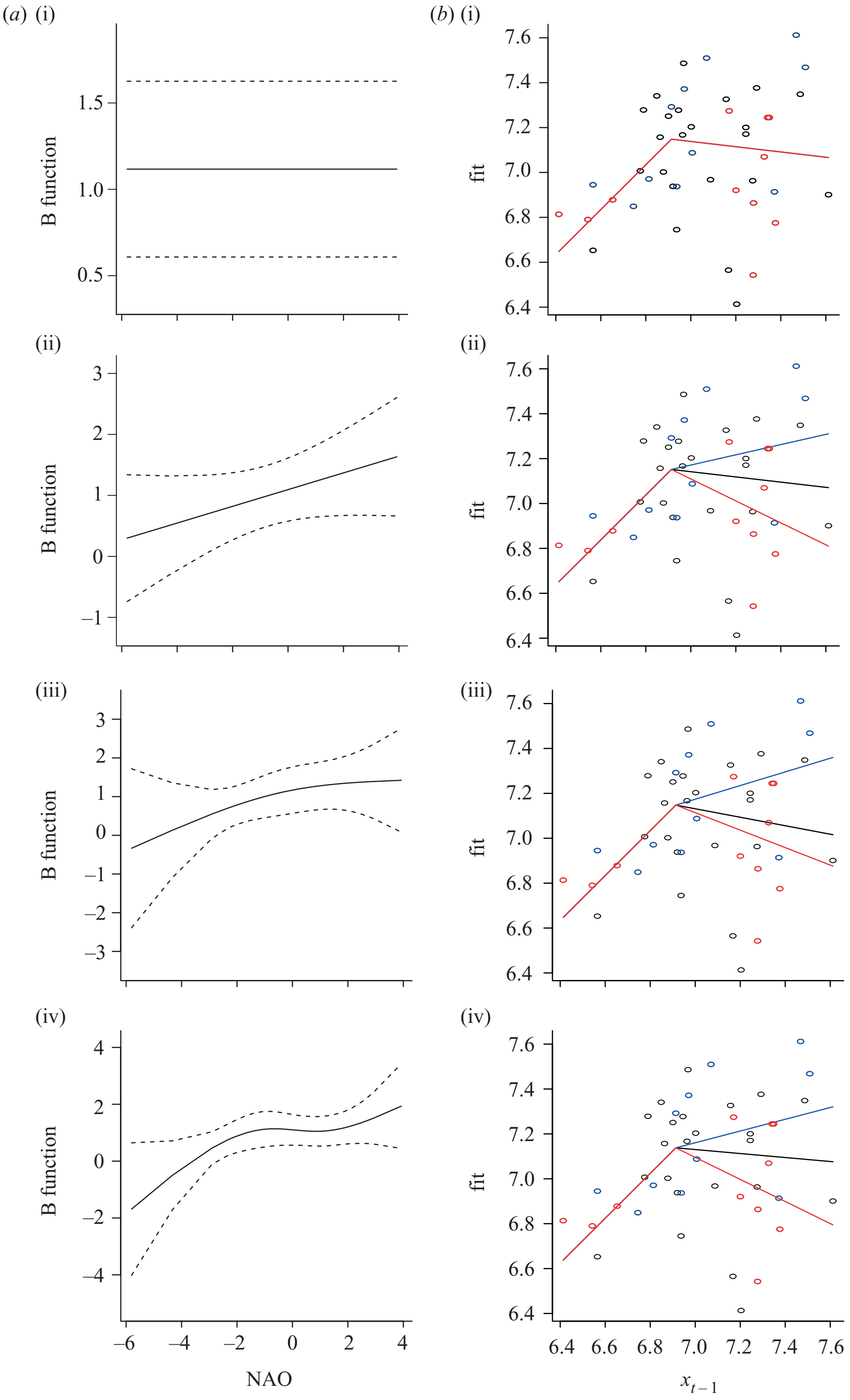

Figure 2. The resulting B(NAO) function (*a*) for various d.f.: (i) d.f. = 1; (ii) d.f. = 2; (iii) d.f. = 3; (iv) d.f. = 4, and (*b*) the corresponding phase plots with the original data inserted together with the resulting FCTAR model for (in the case of d.f. $\geqslant 2$) three levels of (detrended) NAO: blue line corresponds to NAO = −2.79; black line corresponds to NAO = −0.310; and red line corresponds to NAO = 2.84. The model given by equation (4.1) assumes a smooth transition, whereas the TAR model assumes a continuous but non-differentiable instantaneous transition. For the log-transformed Soay sheep data, the FCTAR (AIC = −124.7, $R^2 = 10.3\%$, adjusted $R^2 = 6.1\%$) provides a better fit than the MSS model (i.e. model (4.1)) (AIC = −107.2, $R^2 = 6.9\%$, adjusted $R^2 = 2.5\%$). For the Soay sheep data, model (1) approximating the TAR model is given by $R_0 = 1.26$, $b = a_1 - a_2 = 1.17$ 3 and K = 1006, whereas the best-fitted model (1) has the parameter estimates being $R_0 = 1.93$, $b = 1.763$. and $K = 1270$. In particular, for a value of b of *ca.* 1, the TAR model and the MSS model do not resemble each other closely around the threshold (k), although they approach each other asymptotically for values distant from k.

Table 2. Empirical frequency of d.f. selected when the simulated time-series are generated (*a*) by the ASMM and (*b*) by the Constrained FCTAR model.

(The number of replications is 1000. In (*a*) the (centred) NAO are iid normally distributed with zero mean and standard deviation equal to $c \times 0.2$ (roughly that of the observed NAO series); *c* parameterizes the strength of the NAO effect. In (*b*) the (spline-detrended) NAO are iid normally distributed, with mean and standard deviation equal to -0.102 and 2.01, respectively (the observed values over the study period). In both cases, when the effect of the NAO is present in the simulations, the new time-series method is able to detect it with high probability. (Numbers in bold are the frequencies of the cases whose estimated d.f. coincide with the true d.f.; in (*b*), since there is a tendency to over-fit the degrees of freedom, it is appropriate to compare those with estimated d.f. $= 1$ (i.e. no effect of the NAO) and those with estimated d.f. $\geqslant 2$ (i.e. estimated effect of the NAO). Italics represent entries within which we would expect the majority of the simulated cases to fall, if the time-series method properly picks up the effect of the NAO. Bold figures represent the majority-cases.))

(*a*) the ASMM simulations

	d.f.			
c	1	2	3	4
1 ($n = 50$)	0	*6*	***466***	***528***
0.75 ($n = 50$)	0	*40*	***417***	***543***
0.50 ($n = 50$)	0	*232*	***328***	***440***
0.25 ($n = 50$)	3	***515***	***239***	*243*
0.01 ($n = 50$)	***429***	257	159	155
0.00 ($n = 50$)	***601***	160	123	116
0.00 ($n = 200$)	***624***	143	115	118

(*b*) the constrained FCTAR simulations

		estimated d.f.				
sample size	true d.f.	1	2	3	4	$\geqslant 2$
50	1	***685*** *(69%)*	149	89	77	315
200	1	***776*** *(78%)*	110	63	51	224
50	2	263	***503*** *(50%)*	130	104	*737 (74%)*
200	2	6	***768*** *(77%)*	150	76	***994*** *(99%)*

range of free-living populations across several taxa are influenced by climate—regardless of whether they are resource- or predator-limited (Stenseth *et al.* 2002). Previously, we considered only *b* to be a function of the NAO, although it is plausible that this may also be true of the other two ecological parameters, *k* and *r*. If either *k* or *r* is a function of the NAO, the intercept term a_0 must be a function of the NAO, in which case the NAO also affects the system through an additive component besides its non-additive effect through the parameter *b*. We have also fitted a FCTAR model with both a_0 and a_2 as spline functions of the NAO, but a constant a_0 is selected by AIC. This does indeed suggest that the NAO affects the Soay sheep dynamics mainly through the parameter *b*.

In common with other time-series techniques, the power of the FCTAR method depends on the signal-to-noise ratio, as well as the sample size. With the increasing awareness of the value of long-term data (including count data), we are convinced that the FCTAR method will prove applicable for a variety of systems, and thus provide indications of interesting biological insight. It is certainly encouraging to note that, for the Soay sheep system, the inferential FCTAR time-series approach identified similar nonlinear, non-additive climate–density interactions as proposed by Coulson *et al.* (2001) using a more deductive, process-oriented approach. For age-structured systems, the strongest climatic signal may be embedded in some intra-group transitions, for example, the junior and the senior groups (Gaillard *et al.* 1998). A generalization of the FCTAR approach to modelling intra-group transitions provides a promising approach to detecting climatic effects with otherwise short time-series data.

6. CONCLUSION

We have developed a method that can detect the non-additive and nonlinear ecological effects of climate on population dynamics, which is probably due to the interaction between climate and population density, using only count data. The importance of our model is its ability to detect effects of the NAO on the basis of *only* total population count data. A detailed understanding of the mechanisms that generate nonlinear and non-additive dynamics can only come from the modelling of detailed long-term individual-based data relating to fecundity and survival, or through large-scale experimental manipulations. Not surprisingly, the ASMM with its larger number of parameters and more mechanistic approach, captures the Soay sheep population dynamics with greater accuracy than any of the time-series methods, but the FCTAR method will, using a much simpler model with much less data demand, help to direct attention to those systems being dynamically affected by climate fluctuations. It also allows an examination of the prevalence of such effects in ecological time-series. Our analyses suggest that even small changes might have profound dynamic effects—the latter of which might have cascading effects on entire ecosystems (Post *et al.* 1999). When faced with the threats of global warming, this will be of great value in our efforts to adjust to the resulting ecological changes due to climate change.

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