



Predicting nonlinear and non-additive effects of climate: the Alpine ibex revisited

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ABSTRACT: Climate can have complex effects on demographic rates and the endogenous feedback structure regulating mammal populations, and this can create problems for predictive modelling. In northern and Alpine environments, weather appears to influence ungulate population growth rates mainly during years of high population density, suggesting the possibility of nonlinear interactions between the 2 variables. Threshold models have been employed to account for these nonlinearities. For example, in the case of Alpine ibex *Capra ibex* in the Gran Paradiso National Park of Italy, stronger density dependence is assumed to occur after snowfall exceeds 1.54 m. In this paper we use more objective nonparametric methods to evaluate the form of the functional relationships governing the dynamics of this ibex population. No evidence was found for a threshold effect in the data. Instead we uncovered a non-additive and nonlinear interaction between climate and population density. The resulting models predict ibex numbers as well or better than previous threshold models despite requiring fewer parameters, and also conform well to traditional ecological concepts. We conclude with several lessons for those who wish to predict the effects of climate change on animal population dynamics.

KEY WORDS: Ibex · Population dynamics · Lateral perturbations · Theoretical models

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1. INTRODUCTION

Populations of ungulates in northern latitudes and alpine environments are severely influenced by winter weather and, in particular, by snowy or rainy weather related to years with a high Northern Atlantic Oscillation (NAO) index; e.g. in Soay sheep (Grenfell et al. 1998, Coulson et al. 2001), red deer (Forchhammer et al. 1998, Post & Stenseth 1998), reindeer (Aanes et al. 2000, 2003), roe deer (Grøtan et al. 2005) and Alpine ibex (Sæther et al. 2002, Jacobson et al. 2004). One of the interesting features of many of these ungulate populations is that weather only seems to be important during years of high population density (Grenfell et al. 1998, Jacobson et al. 2004), suggesting the possibility of non-additive and/or nonlinear interaction between the 2 variables. One solution to this problem is to separate the effects of weather or density by a

threshold. For instance, Jacobson et al. (2004) used a snow-depth threshold to separate the Alpine ibex data into years of high and low snow depth and then estimated different linear models for each data set. In contrast, Grenfell et al. (1998) and Stenseth et al. (2004) used a population density threshold to separate Soay sheep data into high and low density years and then assumed that winter weather only affected the high density group. A problem with this approach is that the threshold appears to be more an artefact erected to enable statistical analysis than a real biological phenomenon, which makes it difficult to interpret results within a meaningful theoretical context. In this paper we take a more objective, nonparametric approach to model selection and diagnosis and, as a result, find no evidence for a threshold in the Alpine ibex data. Instead, we found that a simple nonlinear logistic model, in which snow depth acts as a lateral perturba-

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tion (Royama 1992) on the ibex regulation function, describes the data equally well but with fewer parameters. This model provided an ecological explanation for the non-additive and nonlinear interaction between climate and density, and predicted changes in ibex numbers as well or better than previous models.

2. MODEL OF JACOBSON ET AL. (2004)

Jacobson et al. (2004) analyzed the Alpine ibex *Capra ibex* census from 1961–2000 in Gran Paradiso National Park, Italy (Fig. 1A) using the linear model

$$y_i = a + bn_i + cv_i + en_i v_i + \sigma \varepsilon_i \quad (1)$$

where y_i is the realized logarithmic per capita rate of increase ($x_{i+1} - x_i$), x_i is the natural logarithm of n_i , the size of the population measured in the autumn of year i , v_i is the maximum depth of snow (Fig. 1B) during the following winter, a , b , c and e are parameters estimated by regression, and residuals ε_i are assumed to be normally distributed with standard deviation σ . They also employed a log-linear model in which n_i in Eq. (1) is replaced by its natural logarithm x_i . Preliminary graphical analysis led the authors to propose a threshold effect in which the density feedback was more intense (steeper) in years when snowfall >1.54 m (Fig. 2). Separating the 39 yr of data (1961–2000) into 2 groups according to this threshold, they then fit linear (and log-linear) models for Eq. (1) to each group (NB population data from 1956–1960 were omitted because of absence of snow data). Threshold models generally gave better descriptions of the data than other linear models, with the best of them explaining around 80% of the variation in y_i .

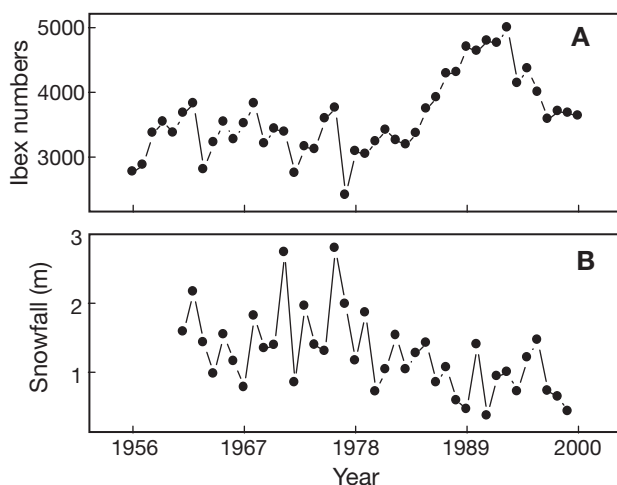


Fig. 1. (A) Total population of Alpine ibex *Capra ibex* in Gran Paradiso National Park, Italy, in autumn and (B) maximum snow depth observed during the preceding winter

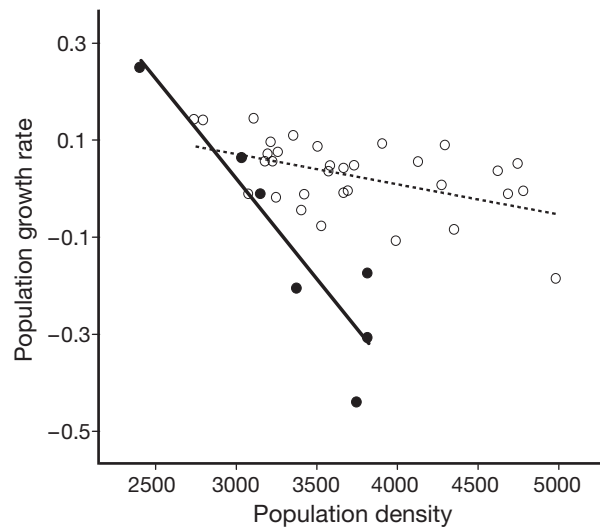


Fig. 2. Per capita population growth rates of Alpine ibex as a function of total population density. Solid and open circles: years when the annual average winter snow depth was >1.54 m and ≤ 1.54 m, respectively

In order to test their models, Jacobson et al. (2004) fit them to data for the first 20 yr (1961–1980) (Table 1, Model A), and then predicted ibex numbers for the next 19 yr. In general, the better threshold models captured some important features of ibex dynamics, particularly the increasing trend during the 1980s (Fig. 3, Model A).

3. NONPARAMETRIC DIAGNOSIS

Rather than making *a priori* assumptions about the form of the population regulation function, we used a diagnostic approach to detect clues in the data. For example, one way to achieve a relatively unbiased view of the form of the functional relationships is to analyze a nonparametric version of Eq. (1)

$$y_i = a + b(n_i) + cv_i + en_i v_i + \sigma \varepsilon_i \quad (2)$$

where b , c and e are now unspecified functions of the independent variables. Statistical analysis was performed in the R environment (R Development Core Team 2004; www.r-project.org) using the Generalized Additive Modeling (GAM) approach of Hastie & Tibshirani (1990). The forms of the functions b , c and e were determined by fitting natural cubic splines to the complete 39 yr of data (e.g. see Bjørnstad et al. 1998), and the complexity of the curve (the number of degrees of freedom) was determined by penalized regression splines and generalized cross validation (GCV) (Wood 2001). Smoothing terms were estimated using penalized regression splines with parameters selected by GCV. Results are summarized in Table 1B.

Table 1. Parametric and nonparametric models fit to the Alpine ibex time series (Jacobson et al. 2004) using methods discussed in Section 2. AIC: Akaike information criterion; GCV: generalized cross validation score; DET: coefficient of determination; n_i : population density in year i ; v_i : snow depth in meters; y_i : $\ln [n_i / (n_i - 1)]$; df: estimated degrees of freedom of the spline term; convex: downward curving; concave: upward curving

Models	AIC	GCV	DET
A. Jacobson et al.'s parametric threshold model (D 13) fit to first 20 yr of data	-48.29		0.91
$y_i = 0.25 + 0.0020 v_i - 0.0108 (n_i \times v_i)$ if $v_i < 154$ cm			
$y_i = 0.25 + 0.0042 v_i - 0.017 (n_i \times v_i)$ if $v_i > 154$ cm			
B. Nonparametric models fit to 39 yr of data			
B1. $y_i = b(n_i; \text{df} = 2.1, \text{convex}) + c(v_i; \text{df} = 1.0, \text{linear}) + e(-n_i \times v_i; \text{df} = 2.3, \text{convex})$		0.005	0.75
B2. $y_i = c(v_i; \text{df} = 1.00, \text{linear}) + e(-n_i \times v_i; \text{df} = 2.30, \text{convex})$		0.0048	0.74
B3. $y_i = e(-n_i \times v_i; \text{df} = 2.43, \text{convex})$		0.0069	0.64
B4. $y_i = b(-n_i; \text{df} = 2.52, \text{concave}) + c(-v_i; \text{df} = 2.09, \text{convex})$		0.0062	0.68
C. Our parametric models fit to first 20 yr of data			
C2. $y_i = -0.015 + 0.37 v_i - 3.05 \times 10^{-6} (n_i \times v_i)^{1.41}$	-62.27		0.93
C3. $y_i = 0.11 - 9.80 \times 10^{-11} (n_i \times v_i)^{2.43}$	-40.39		0.78
C4. $y_i = 0.84 - 9.17 \times 10^{-5} (n_i)^{1.11} - 0.010 (v_i)^{3.45}$	-45.72		0.86

The full nonparametric Eq. (2) explained 75% of the variation in Alpine ibex annual per capita rates of change (see Model B1 in Table 1). The forms of the partial functions are illustrated in Fig. 4 (Model B1). Notice the neutral effect of the b -function (Model B1, independent density effect), the linear positive c -function (Model B1, independent snowfall effect), and the convex negative e -function (Model B1, density acting jointly with snowfall). Not surprisingly, the removal of the b -function had almost no effect on model determination (Table 1, Model B2) or the shape of the c - or e -functions (Fig. 4, Model B2). Removing the b - and c -functions results in a univariate model (e -function) that

resolves 64% of the variation (Model B3, Table 1) and has a convex negative shape (Fig. 4, Model B3). Finally, removing the e -function produces a bivariate model with concave negative b -function and convex negative c -function (Fig. 4, Model B4) that resolves 68% of the variation (Table 1, Model B4). In agreement with Jacobson et al. (2004), our nonparametric analysis indicates that the conjunct variable ($n_i \times v_i$) explains more of the variation in ibex per capita rates of change than any other single variable. However, we found no evidence of a snow-depth threshold. Instead, we uncovered a strongly nonlinear interaction effect, with a pronounced downward curvature (convexity) (see the

e -functions in Fig. 4). Our analysis further suggests that snowfall often has an independent positive linear effect on ibex per capita rates of change (see the c -functions in Fig. 4, Models B1 to B3), a relationship that is difficult to rationalize on biological grounds. It is feasible that increasing snowfall results in higher forage production in the following growing season, but the effect of snowfall is convex negative in Model B4, suggesting the opposite. Notice that, when population density and snow depth are entered as separate variables (Model B4), they resolve somewhat more of the variation than when employed as a conjunct variable, which raises questions about the true nature of the relationship between population density and snow depth; i.e. whether they act on per capita rates in conjunction (Model B3) or as separate, independent effects (Model B4).

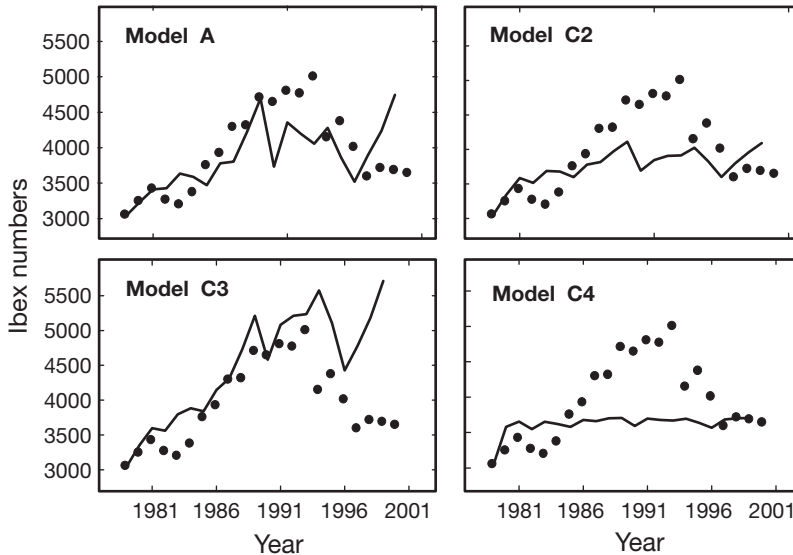


Fig. 3. *Capra Ibex*. Comparison of observed Alpine ibex counts (points) with deterministic predictions (lines) for parameterized models (Table 1). Models fit to data from 1961–1980. Runs began with an initial population size of 3412 ind., the number counted in 1981

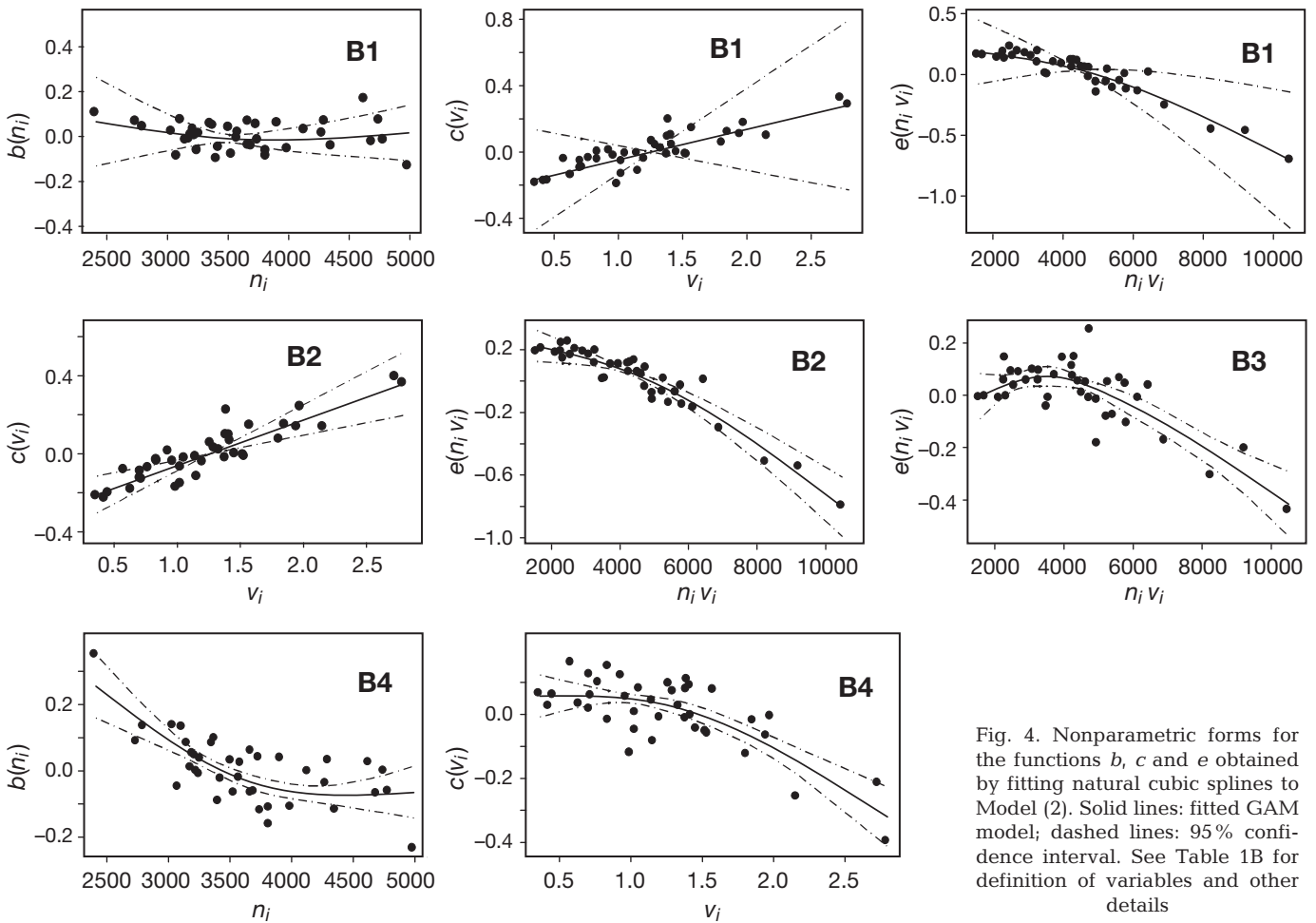


Fig. 4. Nonparametric forms for the functions b , c and e obtained by fitting natural cubic splines to Model (2). Solid lines: fitted GAM model; dashed lines: 95% confidence interval. See Table 1B for definition of variables and other details

4. PARAMETRIC MODELLING

Nonparametric analysis suggests that we should employ a nonlinear model to describe Alpine ibex population dynamics. One possibility is a nonlinear variant of Eq. (1)

$$y_i = a + b(n_i)^\alpha + c(v_i)^\beta + e(n_i \times v_i)^\theta + \sigma \epsilon_i \quad (3)$$

which reduces to the linear Eq. (1) when all power parameters (α, β, θ) are unity, and which approximates the log-linear model as the power parameters become very small. We fit variants of this model to the first 20 yr of data so that we could, like Jacobson et al. (2004) use the last 19 yr to test predictions. Models were fit by nonlinear regression using the *nls* library in the R program (Bates & Watts 1988, R Development Core Team 2004, available at www.r-project.org). Parameter values are given in Table 1C.

Since the b -function contributes nothing to model resolution we ignore this component. A nonlinear model containing the c -function (snowfall acting independently and positively) and e -function (combined

negative effect of snowfall and density) explains >90% of the variation in the first 20 yr of data (Table 1, Model C2), which is comparable to Jacobson et al. (2004) Model D13 (Table 1, Model A), but with 2 fewer parameters (as reflected by the smaller Akaike's Information Criterion [AIC]). However, this model does not effectively predict the increasing trend in ibex numbers during 1983–1993 (Fig. 3, Model C2; correlation between observed and predicted values from 1983–1993 = 0.78). In contrast, a model containing the e -function alone resolves only 78% of the variation (Table 1, Model C3), but makes much better predictions of the increasing trend (Fig. 3, Model C3; correlation between observed and predicted values from 1983–1993 = 0.93). Thus, the independent positive effect of snowfall in Model C1 (c -function) may be spurious and should probably be ignored. Finally, a model representing the independent effects of density and snow depth (i.e. omitting the conjunct variable) resolves 86% of the variation (Table 1, Model C4), but must be rejected for its complete inability to predict the increasing trend in ibex abundance (Fig. 3, Model C4;

correlation between observed and predicted numbers from 1983–1993 = 0.62). Note that the best threshold model of Jacobson et al. (2004) fails to improve on prediction, even though it has 2 more parameters than Model C3 (Fig. 3, Model A; correlation between observed and predicted numbers from 1983–1993 is 0.88). Also note that Models A and C2 both fail to reproduce the peak ibex numbers (almost 5000 ind.) in the years 1991–1993, and that none of the models anticipate the decline in ibex numbers from 1994 to 1997, or the relatively constant numbers during the last 4 yr (Fig. 3). Even though the years 1998 to 2000 had some of the lowest snowfalls on record, the ibex population failed to respond to these favorable conditions, suggesting that a new factor or process may have entered the picture.

5. THEORETICAL INTERPRETATION

Our reanalysis of the Alpine ibex time series suggests that population dynamics in Gran Paradiso National Park over the period 1961–1993 can be described and predicted by a simple nonlinear model with the independent variable being the combined effect of population density and snow depth (i.e. Model C3 in Table 1)

$$y_i = a + e(n_i \times v_i)^\theta \quad (4)$$

However, questions remain about the theoretical interpretation of this model. We can approach the problem by solving Eq. (4) for $y_i = 0$ and $n_i = k$, the size of the population at equilibrium, given $a > 0$ and $e < 0$, the necessary conditions for a stable solution with positive k ; i.e.

$$0 = a - e(k \times v_i)^\theta \quad (5)$$

$$k = \frac{(a+e)^{1/\theta}}{v_i} \quad (6)$$

The equilibrium abundance k (frequently referred to as the carrying capacity of the environment) is inversely proportional to winter snow depth, v_i . Since carrying capacity is usually determined by a limiting factor such as food or space (Leslie 1948, Berryman 1999, 2004), this suggests that the limiting factor is inversely related to snow depth. One possibility is that snowfall reduces the area available for winter grazing (Sæther et al. 2002), a view supported by observations that ibex prefer sun-exposed habitats without snow (Nievergelt 1966) and that large groups of ibex often gather on these preferred areas during years of deep snow and high population density (Toigo 1999). Another possibility is that deep snow increases the maintenance energy demands of individual ibex so that, in years of deep snow and high ibex numbers,

many starve because their energy demands cannot be met. This appears to be the mechanism operating in a Soay sheep population on the island of Hirta (Berryman & Lima 2006).

The above interpretation seems to conform well to classical ecological theory, since, if $[(a/e)^{1/\theta}]/k$ is substituted for v_i in Eq. (4), we obtain

$$y_i = a \left[1 - \left(\frac{n_i}{k} \right)^\theta \right] \quad (7)$$

which is a nonlinear version of the classic logistic model, sometimes called the theta-logistic (see e.g. Verhulst 1838, Richards 1959, Nelder 1961, Gilpin & Ayala 1973, Berryman 1999).

6. PREDICTING EFFECTS OF CLIMATE CHANGE

Our reanalysis of the Alpine ibex time series leads to some important lessons concerning the prediction of climatic effects on population dynamics. The first is that the structure of the model is of critical importance (Berryman 1992). For instance, if we only had data from 1961–1980 and had assumed, like many before us, that climate has an additive effect on the rates of population change, we would have ended up with a model that was incapable of predicting the increase in ibex numbers over the following years (e.g. Model C4). Additive climatic effects cause what Royama (1992) calls vertical perturbations to the growth function, while interactions between climate and density cause lateral perturbations (e.g. Model C3). These different kinds of perturbations can have very different consequences for population dynamics (cf. Models C3 and C4 in Fig. 3). Moreover, the ecological mechanisms underlying lateral perturbations imply that the exogenous factor (snow depth) influences a resource such as food or space (Berryman 2004). Although, other studies have shown that snow depth and winter weather affect Alpine ibex population dynamics (Sæther et al. 2002, Jacobson et al. 2004), our results suggests that they probably act on the carrying capacity, a hypothesis that had not been proposed previously. The lesson is clear: it may be misleading, or even dangerous, to make *a priori* assumptions about the structure of the underlying model (Berryman 1992).

The second lesson emerging from our study is that the usual criteria for model selection may not be good enough. It is common to see models selected on the basis of coefficients of determination ($DET = r^2$) or AIC (Burnham & Anderson 1998). If our results can be extended to other situations, it seems that these criteria may not be effective at selecting models with good predictive capabilities. For instance, Model C2 had the best AIC and DET (Table 1) but was unable to pre-

dict the ibex population increase (Fig. 3). In contrast, Model C3 with its much less impressive AIC and DET was able to capture this trend with one parameter fewer (Table 1, Fig. 3). From this we conclude that the only real way to judge and compare ecological models with any degree of confidence is in their ability to predict independent observations. Thus, some of the available data should be saved for testing model predictions. Here we are again in agreement with Jacobson et al. (2004).

The third lesson comes from the inability of all models to predict the decline and apparent stabilization of ibex numbers following the peak in 1993. It is clear that climate can affect many components of the ecosystem, some of which may be unknown or unmeasured (e.g. food, predators, competitors), but which can affect the variable(s) of interest. For instance, chamois *Rupicapra rupicapra* also increased in Gran Paradiso National Park, in a similar way to the ibex, but did not decline during the final years (A. Provenzale pers. comm.). Thus, one could speculate that inter-specific competition with chamois may have been at least partly responsible for preventing continued growth of the ibex population. The fact that chamois seem to do better in the more favorable habitats (Forsyth & Hickling 1998), and that the availability of such habitats is likely to increase with decreasing snow depths, may support this proposition. Once again the lesson is clear: accurate forecasts of climatic effects may require multi-species time series data and multi-species models, and for this we will need to broaden our sampling to include as many environmental components as possible.

Finally, we need to briefly comment on the nonlinear diagnostic approach employed in this paper. Although nonparametric techniques like GAM offer a relatively unbiased way to deduce the form of functional relationships, they are not a panacea. Statistical probes should generally be used with caution, and can never substitute for biological and ecological knowledge and insight (see, e.g. Berryman & Turchin 1997, 2001). In addition, it is important to emphasize that we only used the GAM approach for diagnostic purposes, not for constructing predictive or explanatory models, which we feel should have an ecological derivation; i.e. as with the logistic equation (Royama 1992). It is comforting that, although we did not start out with any particular ecological model in mind, we ended up, after an objective assessment of the data, with the familiar nonlinear logistic.

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