

Deciphering the Effects of Climate on Animal Populations: Diagnostic Analysis Provides New Interpretation of Soay Sheep Dynamics

Alan Berryman^{1,*} and Mauricio Lima^{2,†}

1. Departments of Entomology and Natural Resource Sciences,
Washington State University, Pullman, Washington 99164;

2. Center for Advanced Studies in Ecology and Biodiversity,
Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago,
Chile

Submitted October 19, 2005; Accepted July 5, 2006;

Electronically published October 12, 2006

Online enhancements: appendixes.

ABSTRACT: Soay sheep on the island of Hirta exhibit periodic population collapses that have been proposed to result from nonlinear interactions between weather, population density, and age structure. Here we employ a diagnostic approach to reanalyze the data from 1985 to 2004 and find that climate mainly affects the equilibrium population size, thus acting as a lateral perturbation. From this, we derive a simple energetic model for a population interacting with its food supply in the presence of variable winter weather. This model explains the strong nonlinearity in the Soay sheep population regulation function and provides a framework for evaluating climatic perturbations. We examined two integrative climatic indexes, one representing effects on forage production and the other representing the severity of winter weather. Results suggest that the latter has the main effect on Soay sheep population dynamics. Models incorporating this variable provided fairly accurate predictions of Soay sheep population fluctuations. The diagnostic approach offers an objective way to develop simple, nonstructured population models that are useful for understanding the causes of population fluctuations and predicting population changes, provided they are based on a careful consideration of the underlying biological and/or ecological mechanisms.

Keywords: population, diagnosis, time series, competition, climate.

* E-mail: aaberryman@msn.com.

† Corresponding author; e-mail: mlima@bio.puc.cl.

Am. Nat. 2006. Vol. 168, pp. 784–795. © 2006 by The University of Chicago. 0003-0147/2006/16806-4137\$15.00. All rights reserved.

Following the groundbreaking work of Royama (1977, 1981, 1992), ecological time series analysis and diagnosis has become one of the fastest-growing areas of population ecology. Perhaps the most studied time series is that for a population of Soay sheep (*Ovis aries* L.), an ancient lineage of domesticated sheep living, unmanaged, on the island of Hirta in the St. Kilda archipelago off northwest Scotland. There are several reasons why this time series is of particular interest. First, it is a closed population, so changes in numbers are completely determined by births and deaths and, therefore, the redistribution of animals in space is not part of the problem. Second, because the census involves counting the entire population, they are quite accurate, at least over the periods 1959–1969 and 1985–2004 (accurate, that is, relative to many other time series found in the literature). Finally, additional information has been collected on individual animals living on one part of the island (Village Bay) since 1985—including sex, age, and parasite load—as well as on the abundance of forage vegetation (Clutton-Brock and Pemberton 2004). If we cannot unravel and explain the causes of numerical fluctuations in this isolated population, what chance do we have with others?

Clutton-Brock et al. (1991) used the approach of Varley et al. (1973) to analyze the data from 1955 to 1967, concluding that the key factor affecting population fluctuations was starvation during winter, particularly among lambs and rams. They also noted that starvation was related to population density in a nonlinear fashion. Grenfell et al. (1992) used simple single-species models with and without age structure to show that the population fluctuations observed between 1985 and 1991 could be explained by overcompensatory density regulation in age-structured models. Recently, studies have focused on the effect of climate on the dynamics of Soay sheep. Grenfell et al. (1998) analyzed a nonstructured threshold autoregressive model (SETAR) to show that the occurrence of March gales during years of high sheep density increased the probability of a severe population crash, a result sup-

ported by the demographic analysis of Catchpole et al. (2000). Stenseth et al. (2004) used a somewhat different threshold autoregressive model (FCTAR) to conclude that climatic fluctuations, as represented by the North Atlantic Oscillation (NAO; Hurrell 1995; Stenseth et al. 2003), could drive Soay sheep population fluctuations through different dynamical regimes via nonlinear interactive effects. Coulson et al. (2001) employed a structured population model to show that Soay sheep fluctuations could result from different age classes responding differently to climatic variation as a function of their life history. Finally, the age-structured model of Owen-Smith (2002) indicated that Soay sheep population fluctuations could be caused by severe overwinter depression of relatively high-quality food.

At this point, we may well ask whether anything more needs to be said about Soay sheep dynamics on Hirta. Obviously there is, and the reasons are as follows. First, the nonstructured threshold models of Grenfell et al. (1998) and Stenseth et al. (2004) make assumptions about the form of the density feedback (i.e., a threshold effect) that are difficult to justify biologically and leave unanswered questions about the biological mechanisms involved. In addition, these models explain only a small fraction of the total variability in the data, which is hardly comforting. (Adjusted coefficients of determination for FCTAR models are all <13% [Stenseth et al. 2004], partly because of the inclusion of data from 1970 to 1984, which are of dubious precision [Clutton-Brock and Pemberton 2004].) As far as we know, the predictions of these models remain untested.

Second, although structured population models (Coulson et al. 2001; Owen-Smith 2002) may describe the dynamics quite well, they require data on the age and sex of the animals, information that is not readily available for many populations. If knowledge of age and sex structure is indeed necessary to understand and predict fluctuations of animal populations, then many recent publications and most population data would have to be dismissed. Thus, part of our motivation was to demonstrate that simple, nonstructured models can be helpful in understanding the causes of population change and can make reasonably accurate predictions. Unlike many of the analyses seen in the literature, however, we argue that data should be analyzed and interpreted within the context of a sound theoretical framework, and models should be developed with regard to the underlying biological and/or ecological mechanisms involved. Third, no study to date has considered the possibility of climate acting as a lateral perturbation (Royama 1992) on the Soay sheep regulation function, even though circumstantial evidence suggests this possibility. Our reanalysis of the Soay sheep data employs a diagnostic approach (Berryman 1999) to try to

understand how climate affects population dynamics. On the basis of this understanding, we develop a conceptual model for the postulated effects and evaluate two potential climatic indicators. In this way, we arrive at a new interpretation of the effects of climate on Soay sheep and new insights into the mechanisms and interactions underlying their unusual dynamics on the island of Hirta.

The Basic Model

We begin with a simple, nonstructured theoretical model describing the effects of scramble-like competition (as defined by Nicholson 1954) on the dynamics of a population composed of a single species (Royama 1992; Berryman 1999):

$$N_t = N_{t-1} \exp \left\{ R_m \left[1 - \left(\frac{N_{t-1}}{K} \right)^Q \right] \right\}. \quad (1a)$$

For analytical convenience, we write it in terms of the per capita rate of population change:

$$R = \ln \left(\frac{N_t}{N_{t-1}} \right) = R_m \left[1 - \left(\frac{N_{t-1}}{K} \right)^Q \right], \quad (1b)$$

where N_t is the size of the sheep population in August of year t (when the census occurs), R_m is the maximum logarithmic per capita rate of change over a year (i.e., from August of year $t-1$ to August of year t), K is the population size at equilibrium (sometimes called the carrying capacity), Q is a coefficient of nonlinearity, and R is the realized logarithmic per capita change over a year. Equation (1a) is a nonlinear variant of the discrete logistic equation (Cook 1965), commonly called the Ricker model, with the nonlinear parameter Q justified on empirical grounds (Richards 1959; Nelder 1961; Gilpin and Ayala 1973). Equation (1b) describes the process of population regulation by intraspecific competition for resources—what we call the R -function (Berryman 1999). Since this model is different from those used previously to study Soay sheep dynamics, we should explain why we chose it as the basis of our analysis.

First, the pattern of oscillation seen in the Soay sheep on Hirta is typical of overexploitation and collapse resulting from scramble competition. Second, the discrete logistic model derives from first principles consideration of a randomly distributed population competing for a common resource (Royama 1992), an assumption consistent with scramble competition. In contrast, the hyperbolic logistic used in other analyses (Grenfell et al. 1992, 1998;

Stenseth et al. 2004) is considered to be more representative of a population regulated by contest competition (Royama 1992). Although the hyperbolic form is sometimes used to represent scramble situations (Hassell 1975), we prefer a model derived explicitly from first principles. We should add, however, that using the hyperbolic version of the logistic has little or no effect on our results or conclusions.

Methods

Given the basic R -function (eq. [1b]) for the endogenous feedback structure regulating Soay sheep population dynamics, then the effect of exogenous factors can be visualized as follows (Royama 1992).

Vertical perturbation effects. Here the exogenous factor has an additive effect on the total R -function, causing it to deflect vertically with proportional alterations to both R_m and K . Vertical perturbations cause changes in the level of equilibrium, through effects on K , and in the pattern of oscillation around equilibrium, through effects on R_m ; that is, the period of oscillations is determined by the product $R_m Q$ (Berryman 1999).

Nonlinear perturbation effects. Here the exogenous factor affects the curvature of the R -function through the parameter Q . For reasons stated above, nonlinear perturbations affect the pattern of oscillation as well as K .

Lateral perturbation effects. In this case, exogenous factors affect only the equilibrium level K , causing the R -function to deflect laterally along the abscissa (N -axis). Lateral perturbations are normally expected from changes in an essential resource such as food, nesting sites, and so on. (Berryman 1999, 2004). Lateral perturbations do not change the pattern of dynamics around equilibrium since the sensitive parameters R_m and Q are not affected.

Data

Soay sheep have been counted on the island of Hirta since 1959. However, because the counts from 1970 to 1984 are of doubtful reliability (Clutton-Brock and Pemberton 2004), we chose to restrict our analysis to the longest continuous string of reliable data (i.e., 1985–2004; fig. 1; see also app. A in the online edition of the *American Naturalist*). In our opinion, information obtained from a short series of reliable data is more credible than that obtained from a long string containing unreliable data.

The normalized difference vegetation index (NDVI) is a satellite-generated index strongly correlated with the fraction of photosynthetically active radiation absorbed by vegetation. We used the March to September values as an index of annual forage production (Myneni et al. 1997). Since Hirta is too small to obtain a good NDVI reading,

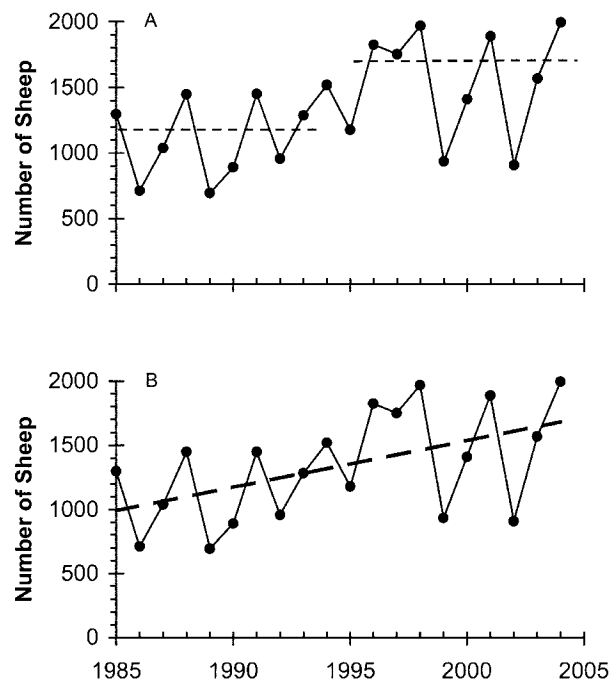


Figure 1: Total counts of Soay sheep on the island of Hirta, showing two hypotheses for the apparent trend in the average number of sheep (dotted lines). A, Step trend. B, Linear trend.

we used values from the Outer Hebrides reported by Durant et al. (2005; see app. A).

The NAO was used as an index of the severity of winter weather (see app. A); for example, a positive NAO is associated with more gales, rainfall, and higher temperatures (Hurrell 1995) and has been previously associated with Soay sheep winter mortality (Catchpole et al. 2000; Coulson et al. 2001; Stenseth et al. 2004).

Analysis

Rather than making a priori assumptions about the structure of the density-feedback function, we employed a diagnostic approach that lets the data direct us toward an appropriate model and its relationship to external perturbations such as climate (Berryman 1999). Analysis was enabled by the population analysis system (see app. B in the online edition of the *American Naturalist*). Nonstationary data were detrended to allow calculation of diagnostic statistics that assist in determining the period of oscillation, the order of the endogenous dynamics (time lags), and the curvature of the R -function. Parameters were estimated by nonlinear convergence (i.e., Marquardt/Newton-Raphson algorithm), and simulations were performed in deterministic and variable environments. Models including climatic

effects were fit by minimizing the Akaike Information Criterion $= -2[\log(\text{likelihood})] + 2(\text{number of parameters})$, using nonlinear regression from the *nls* library in the program *R* (Bates and Watts 1988; see app. C in the online edition of the *American Naturalist*). Models were fit to the sequence from 1985 to 1999 and used to predict the sequence 2000–2005.

Results

Diagnosis

Since the Soay sheep time series is not stationary (fig. 1), the trend was removed by sequencing (i.e., splitting the series into two stationary segments, as in fig. 1A) and linear rotation (i.e., rotating the series around the linear trend in fig. 1B). The two stationary (detrended) series were then used to calculate the statistics (table 1) that led to the following diagnosis (for details, see app. B).

Endogenous Feedback. Mean return times <2 (table 1; see also app. D in the online edition of the *American Naturalist*) and the highly significant negative peak at lag 1 in the partial autocorrelation function (fig. 2A) indicate the presence of strong first order negative feedback, from which we conclude that Soay sheep numbers are probably regulated by intraspecific competition for resources (Berryman 1999). Since starvation is the major cause of sheep

mortality (Clutton-Brock et al. 1991), it seems likely that annual forage production is the resource involved. According to our analysis, endogenous negative feedback accounts for 50%–60% of the variation in observed R values (table 1). These results support our choice of model (1) to describe Soay sheep dynamics and are generally in line with those of previous authors (Grenfell et al. 1998; Coulson et al. 2001; Stenseth et al. 2004).

Exogenous Effects. Systematic linear or step changes in an unknown exogenous factor (climate?) accounted for around 27% of the variation in observed R values (fig. 1; table 1). Although the linear trend accounted for slightly more variability, a deterministic resolution containing the linear trend and endogenous feedback accounted for less variability (79%) than that based on a step trend plus endogenous feedback (85%). In addition, the stability properties and pattern of fluctuations of the step model were more consistent with those observed in the data in both deterministic and stochastic environments (table 1; cf. oscillation periods in the first and last rows). Several clues suggest that exogenous factor(s) acted as a lateral perturbation on the parameter K . First, the parameter K increased by 44%, whereas R_m increased by only 8% over the step trend (table 1; fig. 2B). Since vertical perturbations are expected to cause a proportional increase in both parameters, this explanation seems unlikely. On the other

Table 1: Diagnostic analysis of the detrended Soay sheep time series 1985–2004

Statistic	Linear detrended	Step detrended ^a
Oscillation period	3.167 $\pm$.373	3.167 $\pm$.373
Return time ^b	1.015 $\pm$.442	.975 $\pm$.372
Parameters estimated for model (1):		
R_m	.606	.444 (.416; .450)
Q	2.878	5.189 (5.258; 9.211)
K	1,399	1,716 (1,220; 1,756)
$100r^2$	70.65	79.70
Variation explained ($100r^2$; %):		
Exogenous trend	27.28	26.08
Endogenous feedback ^c	51.38	58.91
Total deterministic model	78.66	84.99
Residual random variability	21.34	15.00
Stability properties:		
Deterministic ($R_m Q$) ^d	1.74 (damped stable)	2.3 (2-year cycle)
Stochastic (oscillation period) ^e	2.53 $\pm$.794	2.80 $\pm$.938

Note: See appendix B in the online edition of the *American Naturalist*.

^a Numbers in parentheses are statistics for each sequence (1985–1994 and 1995–2004).

^b Average time taken to return to the mean following a displacement from the mean (see app. D in the online edition of the *American Naturalist*).

^c Calculated as variation not explained by trend (i.e., $100 - 27.28$) times variation explained by model fit to detrended data (i.e., 70.65) divided by 100.

^d Deterministic stability of equation (1) is determined by the product $R_m Q$ (Berryman 1999).

^e Stochastic oscillation period determined by simulation of the model in randomly varying environment, that is, by adding a standard normal deviate with standard deviation 0.1 to the deterministic R calculated from the model.

hand, Q increased by a large amount (75%), which suggests a possible nonlinear perturbation effect. However, such a large increase in Q without a corresponding decline in R_m (which was not observed) should cause a noticeable increase in the period of oscillation (which was also not observed in the data; see fig. 1). In contrast, exogenous effects on K would cause changes in the average level of abundance without influencing the period of oscillation. It is worth noting that the typical pattern of 3-year oscillations seen in the data (fig. 1) is possible only over a very limited range of the parameter combination $R_m Q$ of model (1); that is, strict 3-year oscillations are seen only when $3.1 < R_m Q < 3.24$. In stochastic environments, this criterion is even more restrictive. Thus, it seems highly unlikely that the observed changes in Soay sheep dynamics can be explained by environmental factors that affect R_m or Q . The final clue comes from the observation that food is likely to be the limiting factor on Hirta (Clutton-Brock et al. 1991; Crawley et al. 2004), and food is known to mainly affect K without influencing the other parameters (see, e.g., Berryman 2004).

Modeling

Accepting, for the purpose of argument, that exogenous factors operate as a step function (fig. 1A), then we can separate the data into two sequences (1985–1994 and 1995–2004) and fit nonlinear R -functions (eq. [1b]) to each approximately stationary sequence (fig. 2B; see also app. B). Notice how both R -functions have strongly down-curving or convex shapes because of large Q values (i.e., $Q \gg 1$), as does the model fit to the detrended series (table 1). It is not clear, however, why they have this shape and what role climate plays in it. To understand this requires us to think more deeply about the interaction between population size, food supplies, and winter weather.

Since the production of food plants on the island during a given year is expected to determine, along with population size, the amount of food available to an average sheep (Illius and Gordon 2000; Crawley et al. 2004), then the food (or energy) accumulated by an individual during that year should approach some maximum level (the energy demand, E_m) as food becomes very abundant or the population becomes very sparse. A simple way to express this is

$$E = E_m - \frac{N}{bF}, \quad (2)$$

where F is the total amount of forage produced during the year and b measures the efficiency of conversion of available food into utilizable energy. Note that the energy gained can be negative if F is small or N is large, in which

case the average animal can lose energy (or weight). This simple model is probably reasonable as long as the total amount of forage produced in a given year does not approach 0 (which seems an unlikely event). In addition, the use of more complicated models does not substantially affect our argument.

We now try to imagine how winter weather can affect this relationship. Suppose an animal needs to acquire E_w units of energy to survive a winter of severity W , then the probability of that individual dying during that particular winter can be defined as

$$D = \begin{cases} 0; & E \geq E_w \\ 1; & E < E_w \end{cases}. \quad (3)$$

Furthermore, following the reasoning above, we can say that there is a particular population size N_w that would gain exactly E_w units of energy from any given level of forage production F :

$$E_w = E_m - \frac{N_w}{bF}, \quad (4)$$

and, therefore,

$$N_w = bF(E_m - E_w). \quad (5)$$

Notice that this particular population size varies according to the energy gain needed to survive a given winter (E_w) and the food produced during the growing season (F), both of which could be related to climate. This is quite important since it provides a natural framework for introducing the effects of weather into our model.

Returning to equation (3) and substituting equations (2) and (4) for E and E_w lead to a death function expressed in terms of population size rather than energy:

$$D = \begin{cases} 0; & N \leq N_w \\ 1; & N > N_w \end{cases}. \quad (6)$$

This D -function assumes that all animals obtain the same amount of food and require the same amount to survive winter, an assumption that we will relax later. Under these conditions, N_w defines a critical population size above which all animals die and below which all survive (fig. 3A), given a winter of severity W . We can translate this into an R -function by noting that $R = \ln[1 + B(1 - D_l) - D_a]$, where B is the per capita annual birth rate and D_l and D_a are the probabilities of death for lambs and adults, respectively (Berryman 1999). Assuming, without loss of generality, that the death rates for lambs and adults are equal, then we see that $R = R_m$ when $D = 0$ and $R = -\infty$ when $D = 1$ (fig. 3B). (Note that the condition

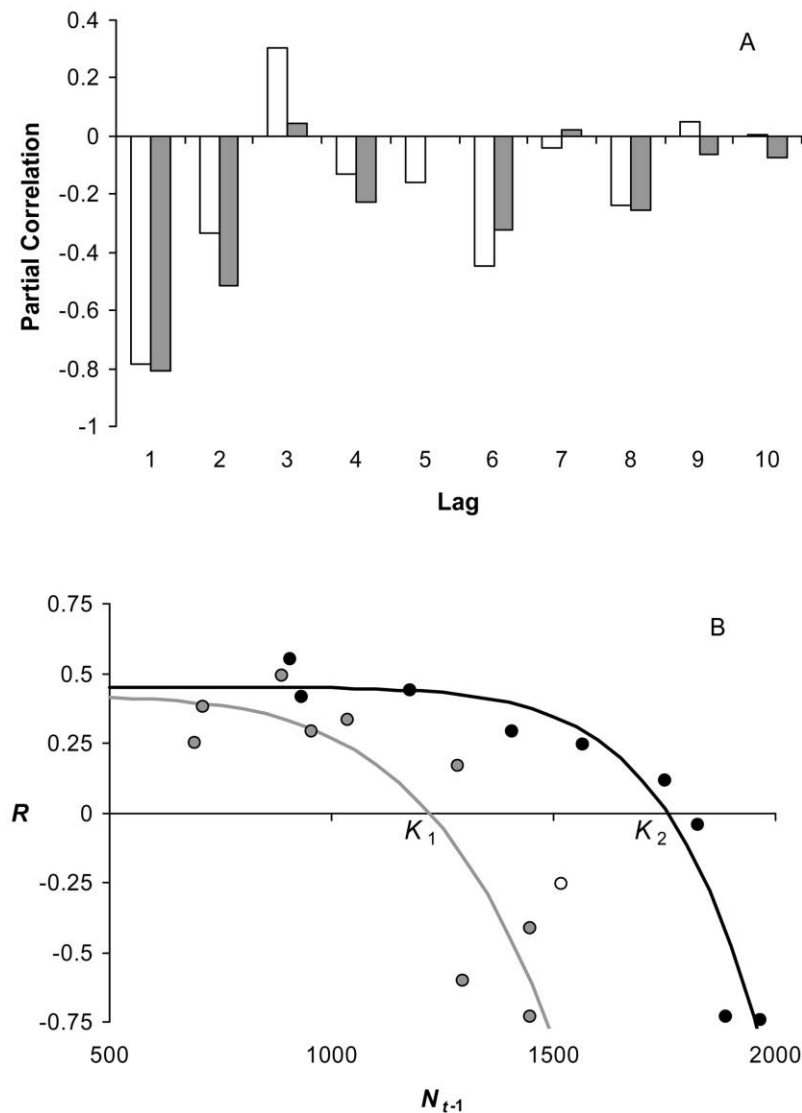


Figure 2: A, Partial correlation between R and N_{t-d} , with d the lag in the feedback response, for Soay sheep data detrended by linear regression (open bars) and by sequencing (gray bars). B, R -functions (eq. [1b]) fit to data from 1985–1994 (gray) and 1995–2004 (black), with an open point for the transition year. See table 1 for statistics and appendix B in the online edition of the *American Naturalist* for methods.

$R = -\infty$ means that all animals die within the interval of observation, in this case a year.) From figure 3B, we see that the equilibrium level K is, in fact, equal to the critical population density, so equation (5) can be written as

$$K = bF(E_m - E_w). \quad (7)$$

Since both F and E_w could be affected by climate while E_m is a species-specific constant, we can write the following model for K as a function of our two climate indices:

$$K = F(\text{NDVI})[E_m - W(\text{NAO})], \quad (8)$$

where NDVI and NAO are proxies for forage production and winter severity, respectively.

Of course, the assumptions of equal food partitioning and equal food requirements are unlikely to be true, but this does not change our basic argument. In the case of random food partitioning and a normal distribution of individual food requirements, the D -function is expected to have the sigmoid shape of a cumulative normal probability density function (fig. 3C), and the R -function would be sharply convex (fig. 3D), just like the real data (fig. 2B). Thus, in addition to providing a theoretical link between climate and K , our argument also provides a logical ex-

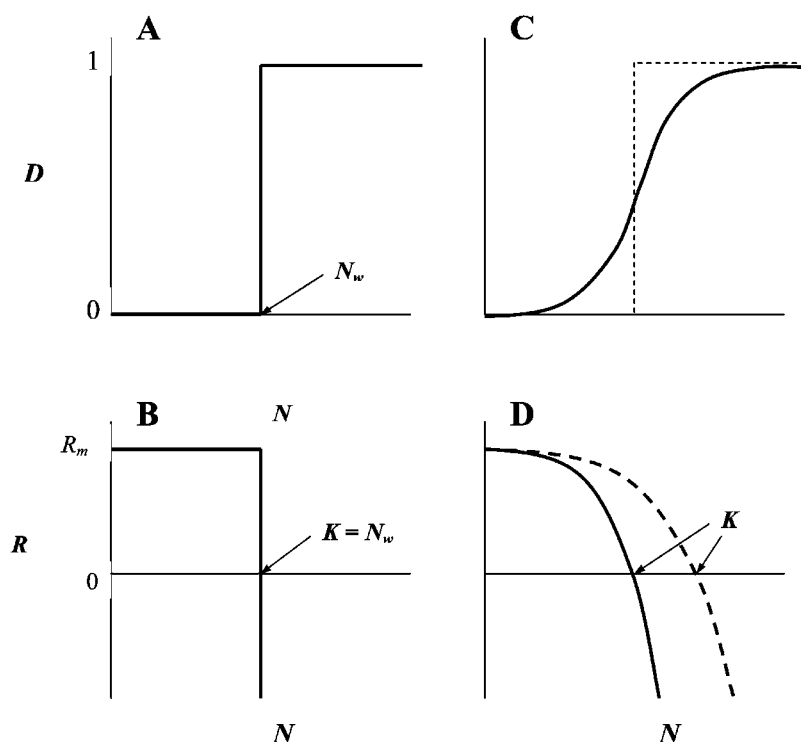


Figure 3: Probability of death (D -function) for Soay sheep under the following assumptions. *A*, Identical individuals obtain the same amount of food and require the same quantity to survive winter; *B*, graph of the corresponding R -function. *C*, Food is randomly distributed among diverse individuals in a population so that the probability of death is now a normal random variable; *D*, graph of the corresponding R -function, showing the effect of a lateral perturbation caused by increased food or decreased winter severity. The variable N_w is the number of individuals that would obtain enough food to survive a winter of severity W given a particular annual supply of forage, and K is the equilibrium population.

planation for the strongly nonlinear form of the Soay sheep R -function.

Evaluating Climatic Effects

The energetic model (eq. [8]) leads to the following hypotheses for the effect of climate on the Soay sheep equilibrium density K : H0, the null model that climate does not affect K , in which case $W(\text{NAO}) = 0$ and $F = \text{constant}$; H1, climate affects K only through forage production, in which case $W(\text{NAO}) = 0$ and $K = F(\text{NDVI})$; H2, climate affects K only through winter severity, in which case $F = \text{constant}$ and $K = K_m - W(\text{NAO})$, with K_m the value of K under the most favorable winter conditions; H3, climate affects K through both forage production and winter survival, in which case $K = F(\text{NDVI})[E_m - W(\text{NAO})]$.

We fit the nonlinear logistic model (eq. [1b]) with K -functions defined by one of the models above to the data from 1985 to 1999 (see app. C), with the remaining data being saved for testing predictions. To maintain simplicity, we assumed that the functions C and W were linear. Pa-

rameters were aggregated so that no K -function had more than two fitting parameters. Parameters were estimated in two ways. (a) Since our diagnostic analysis of the entire data series led to the conclusion that exogenous factors had no effect on the parameters R_m and Q , we set them to the values estimated from the total series after step detrending (table 1; $R_m = 0.444$, $Q = 5.189$). The models were then fit to the 1985–1999 data with these parameters fixed, with the remaining two being estimated by regression. (b) We let all parameters be freely estimated by nonlinear regression. Models were evaluated on the basis of their coefficients of determination, Akaike Information Criterion (Burnham and Anderson 1998), and their prediction of counts from 2000 to 2005 (table 2).

The model H2 with NAO acting alone on K fit the data best (table 2), and model H2a (parameters R_m and Q fixed) provided the best prediction of the observed 3-year population fluctuations (fig. 4). Predictions of this model deviated, on average, <10% (range 2%–25%) from the observed values, while the predictions of all other models were very poor (table 2). We note that the 2005 forecast was made before the sheep count and can therefore be

Table 2: Parameters, statistics, and predictions of the nonlinear logistic (eq. [1b])

Model	R_m	Q	K	DET	AIC	TRA	STP
H0(a)	.444	5.189	1,607.378	.31	17.72	20	61
H0(b)	1.677	.557	1,243.576	.46	3.97	32	65
H1(a)	.444	5.189	$232.283 \times \text{NDVI} + 233.686$	.39	16.66	>100	>100
H1(b)	.916	1.096	$98.792 \times \text{NDVI} + 718.747$	.46	15.77	38	96
H2(a)	.444	5.189	$2,434.365 - 237.315 \times (\text{NAO} + 2.65)$	.63	8.96	10	12
H2(b)	.402	2.916	$2,289.235 - 242.272 \times (\text{NAO} + 2.65)$	.65	9.45	18	18
H3(a)	.444	5.189	$\text{NDVI} \times [444.69 - 44.78 \times (\text{NAO} + 2.65)]$	.58	10.85	>100	>100
H3(b)	.350	3.470	$\text{NDVI} \times [423.76 - 45.41 \times (\text{NAO} + 2.65)]$	.59	11.86	95	333

Note: Logistic with K a constant or a function of the normalized difference vegetation index (NDVI) and/or the North Atlantic Oscillation (NAO), as specified by hypotheses H0–H3. Models were fit to Soay sheep and climatic data from 1985 to 1999 (see app. C in the online edition of the *American Naturalist*). In model a, the parameters R_m and Q are fixed at values obtained from the step-detrended model (table 1), while in model b, all parameters are estimated from these data. DET = coefficient of determination; AIC = Akaike Information Criterion; TRA = mean percent deviation of observed from total trajectory predictions; STP = mean percent deviations of observed from one-step-ahead predictions, calculated as $(\sum |100|O - P|/P)/6$. Boldface values are the parameters of the selected models according to the AIC criteria.

considered a “true prediction.” Total trajectory forecast with model H2a was for 1,434 sheep in 2005 (1,486 with model H2b), while step-ahead forecast was 1,091 sheep (1,249 with model H2b). The actual census was 1,365 sheep.

Discussion

Diagnostic analysis of the Soay sheep time series suggested that climatic factors act mainly on K , causing what Royama (1992) calls a lateral perturbation effect (fig. 5, *top*). Perturbations of this kind have strong effects on the average level of abundance but little on the intrinsic periodicity induced by endogenous feedback. In contrast, previous models assume that climate acts differently when the population exceeds a particular threshold density. In the

SETAR model (Grenfell et al. 1998), climate effects are discontinuous, which makes them difficult to interpret in Royama’s framework (fig. 5, *middle*). In this model, the average level of abundance is affected little by climate, but since endogenous dynamics are “perfectly” stable, population fluctuations are expected to closely follow climatic variations. Under these conditions, we would not expect a strongly periodic component to the dynamics. Finally, the FCTAR model (Stenseth et al. 2004) can be interpreted as a nonlinear perturbation because climate is assumed to affect the steepness of the R -function above the assumed threshold (fig. 5, *bottom*). In this model, climate can have a strong, coincident effect on the average level of abundance and the period of population fluctuations. Since Soay sheep dynamics seem to be dominated by a strongly periodic (3-year) oscillation that does not change appre-

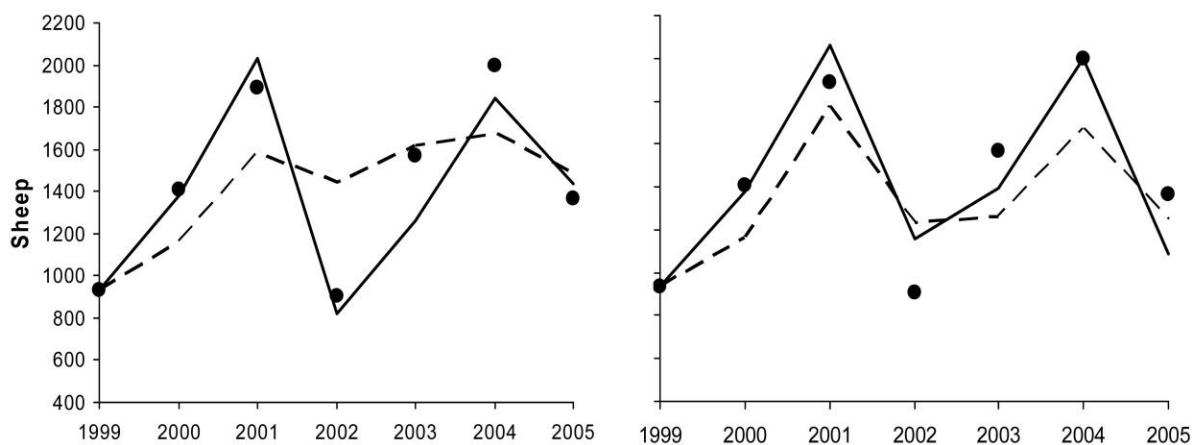


Figure 4: Comparison of observed Soay sheep counts (circles) for the period 1999–2005, with predictions from models H2a (solid line; R_m and Q fixed) and H2b (dashed line; all parameters free) fit to 1985–1999 data. Left, total trajectory predictions initiated with 933 sheep in 1999. Right, step-ahead predictions using real data in year $t - 1$ to predict numbers in year t .

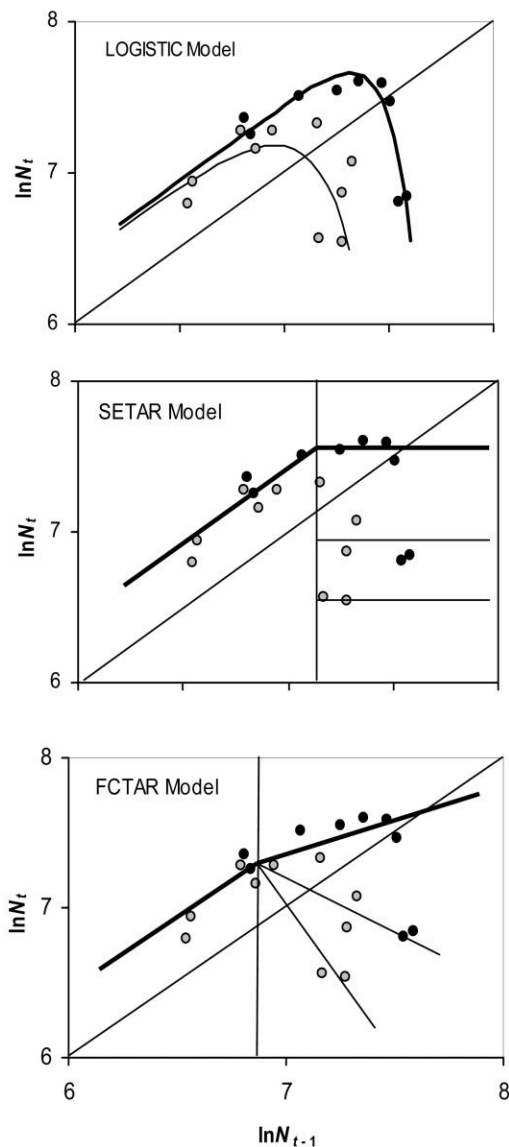


Figure 5: Comparison of maps of single-species, nonstructured models of Soay sheep dynamics and proposed climatic perturbation effects. *Top*, nonlinear logistic model from this article. *Middle*, SETAR model of Grenfell et al. (1998). *Bottom*, FCTAR model of Stenseth et al. (2004). Diagonal 45° line on which $N_t = N_{t-1} = K$ at interception, with the population growth function $N_t = N_{t-1}R(N_{t-1})$. Vertical line indicates the threshold in TAR models. Gray circles, 1985–1994. Black circles, 1995–2004. Thin lines indicate hypothesized effects of climate change.

ciably with respect to average abundance, the data seem to support the interpretation that climate acts as a lateral perturbation on K (fig. 5, *top*)

Lateral perturbations are the result of exogenous factors like climate acting on the population equilibrium (or carrying capacity; Royama 1992). Surprisingly, few analyses

of population dynamics under the influence of climatic change seem to consider this possibility (but see Owen-Smith 2000; Jacobson et al. 2004; Lima et al. 2006). Since equilibrium levels are usually set by a resource in short supply (Berryman 1999, 2004), we should anticipate lateral perturbation effects whenever exogenous factors are suspected of influencing the supply of food or, for that matter, any other essential resource. On Hirta, food is assumed to be the resource in short supply since most of the mortality is from starvation. Hence, explanations of climatic effects on Soay sheep dynamics need to consider the possible effects of climate on food supplies, that is, lateral perturbation effects (Royama 1992). What our study seems to indicate is that total food production does not vary much from year to year but that food requirements for survival can change dramatically in response to variable winter weather. Thus, although equilibrium levels may be set by annual food production, they are modified in unexpected ways by winter weather. In addition, the effects of winter weather are experienced only when the sheep population is close to equilibrium. At other times, winter weather is of little import. It is interesting to speculate that, under such unpredictable circumstances, it would be difficult for sheep to evolve behavioral or physiological mechanisms for avoiding the drastic consequences of overpopulation.

Previous authors have postulated that Soay sheep population dynamics are the result of a nonlinear interaction between climate and population density (Stenseth et al. 2004) and/or population structure (Coulson et al. 2001). Our analysis, however, suggests that the nonlinearity is caused by a fine line (or sharp transition) between having and not having enough food to survive winter; that is, when the population is below this transition point, most animals have sufficient food, while when it is above this point, many do not. This can be thought of as a threshold as long as all animals obtain exactly the same amount of food and have exactly the same energy requirements (i.e., fig. 3*B*). In nature, of course, there is considerable individual variability, and this will result in a more gradual convex relationship (fig. 3*D*). Hence, our model predicts that the sharpness of the transition, or the steepness of the R -function, will be related to variability in resource acquisition and the energy requirements of individuals of different age, sex, and/or social status, as well as variability in food quality (see, e.g., Owen-Smith 2002). In a more general, theoretical context, the form of the R -function seems to be mainly determined by physiological characteristics of the species. For example, a recent theoretical analysis of resource partitioning in single-species populations indicated that convex R -functions are to be expected in species that utilize a large fraction of their total energy consumption for survival and/or have low repro-

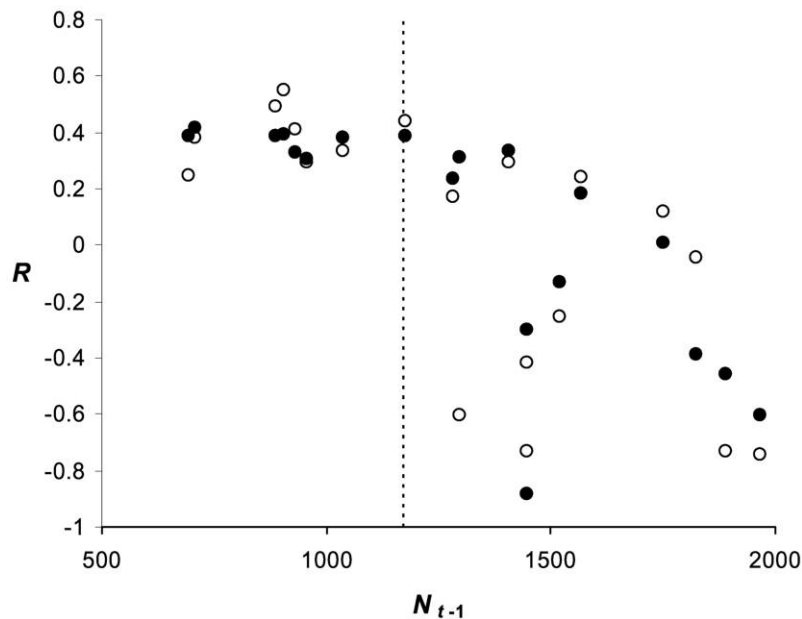


Figure 6: Plot of the per capita rate of change $R = \ln N_t - \ln N_{t-1}$ against the initial population size N_{t-1} for the Soay sheep data from 1985 to 2004 (open circles) and data simulated by model H2(a) (solid circles). Vertical dashed line indicates the approximate “threshold” of the SETAR model.

ductive potentials (K. Johst, A. Berryman, and M. Lima, unpublished manuscript). Since Soay sheep and many other large herbivores possess both of these characteristics, it is not surprising that they also tend to have convex R -functions.

Our interpretation of the Soay sheep R -function seems to be generally in line with that of Owen-Smith (2002). Although Owen-Smith’s model is written in weekly time steps, numerical integration over a year gives rise to a strongly convex R -function (see his fig. 13.7). The reason for this convex shape, according to Owen-Smith, is that high sheep density results in severe overwinter depression of a high-quality food supply, resulting in mass starvation, while a slightly lower density does not reach this critical threshold of food availability. Since our model is based on a discrete annual time step, it cannot be expected to explain seasonal details. What is encouraging, however, is that both models lead to the same general conclusions about the shape of the sheep’s R -function and the resulting population dynamics.

In addition to explaining the nonlinearity in Soay sheep dynamics, the energetic model provides a simple mechanism for incorporating the effects of climate (i.e., through forage production and the critical amount of food [energy] required by an individual to survive winter), providing us with a conceptual framework for evaluating the effects of climate on Soay sheep dynamics (and perhaps other ungulates inhabiting harsh environments). Using NDVI and

NAO as proxies for forage production and winter severity, respectively, we found that the latter had the greater effect on sheep dynamics, supporting the conclusions of previous authors (Clutton-Brock et al. 1991; Grenfell et al. 1992; Coulson et al. 2001). However, the effect of winter weather is not independent or additive but, rather, interacts with food production (see eq. [8]). As far as we know, no previous model considers this possibility explicitly.

Our analysis also demonstrates that simple, nonstructured models can offer reasonable explanations and accurate predictions of structured populations, provided they are based on a sound theoretical framework (see also Owen-Smith 2000), that is, a general analysis of the underlying causal processes within the context of the model structure (Royama 1992; Berryman 1999; Turchin 2003). This is encouraging since most of the available time series data do not include information on age, sex, or spatial structure. Of particular importance in our endeavor was Royama’s classification of exogenous perturbation effects, without which it would have been difficult to visualize the ways in which climate could affect the sheep R -function.

During the extensive review of this article by those involved in the Soay sheep project, several questions arose that required our attention. First, some thought that the trend in the data over the period 1985–2004 could have been caused by a change in the efficacy of counting sheep during this period. If this were true, it would be pretty serious since our whole argument centers on this trend.

However, there are two things that support our view that the trend is real. First, data from the Village Bay subpopulation, which was sampled much more intensively, showed an identical trend, and the two time series were almost perfectly correlated (Clutton-Brock and Pemberton 2004; see their fig. 3.1, 3.2). Since the accuracy of the Village Bay data has not been questioned, we feel that they support the veracity of total population counts. Second, more complicated structured population models with climatic forcing (Coulson et al. 2001) also predict a trend over these years, even though they are not programmed to do so, which also suggests that the trend is real.

There was also some question as to whether our model could reproduce the peculiar pattern seen when the data are plotted in R - N phase space (fig. 6, *open circles*). Notice how variability is low to the left of the vertical broken line and much greater to the right (it was this pattern that motivated the thresholds in SETAR and FCTAR models). Since simulated data seem to produce an almost identical pattern (fig. 6, *solid circles*), we see no reason to reject our model on this basis. We might mention here that this pattern is expected from lateral perturbation effects, which disturb the steeply convex R -function laterally along the N -axis and thereby cause the data to scatter more laterally than vertically.

Also questioned was the number of data points used to estimate parameters of our climatic effect models. The largest number of free parameters in our models was four and the fewest was two, while the number of data points was restricted to 15 (1985–1999) in order to have some data for testing predictions. This leaves us with between four and eight data points per parameter, which is rather low from a statistical point of view. However, our models were deduced from biological principles, so what they may lose in statistical power they may make up for in the power of biological and theoretical insight. It is for the reader to judge which is more important. In the end, of course, it is the predictive and explanatory power of the model that is most important, and our model seems to do quite well on both counts.

Finally, we are obliged to respond to questions concerning the generality of our results. For example, some reviewers thought that our methods would be applicable only to species living on isolated islands with few or no natural enemies. On the contrary, the “diagnostic approach” we used can be applied to any ecological system in which time series are available for one or more species, including those in which natural enemies are important components of the system. Examples can be found in Berryman (1999, 2001, 2002) and Münster-Swendsen and Berryman (2005). Second, the energetic model probably has application to other species that are dependent on resource availability to survive critical periods, including

those in which predation is a major mortality factor; that is, energy reserves may be as critical in escaping from predators as surviving bad weather. Another reviewer wondered whether our analysis has made any significant contribution to general ecological theory. We would turn the question around by saying that our article illustrates how general ecological theory can be employed to understand and explain the causes of population changes in a specific ecological system and to predict future changes in that system. In other words, it is an example of applied ecological theory, in particular, the application of the logistic equation and theories pertaining to nonlinear population dynamics, exogenous perturbations, and resource partitioning. We feel that this is a significant turnaround since theoretical ecology is frequently criticized for its lack of practical applications and predictive power (Peters 1991).

Acknowledgments

We are particularly indebted to T. Coulson, K. Johst, and N. Owen-Smith for their help with the analysis and interpretation of the Soay sheep data and to T. Clutton-Brock, M. Crawley, J. Pemberton, T. Royama, K. Wilson, and several anonymous reviewers for their comments on earlier versions of this manuscript. We appreciate the help of S. Ganguly, Department of Geography at Boston University, for supplying data on the normalized difference vegetation index.

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