

# Phase- and density-dependent population dynamics in Norwegian lemmings: interaction between deterministic and stochastic processes

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We analysed two 26-year long (1970–1995) time-series on annual population growth rates of Norwegian lemmings (*Lemmus lemmus*) from Finse, south Norway, using a threshold autoregressive (TAR) approach. We demonstrate that the population dynamics is both phase- and density-dependent. The phase-dependence accounts for the observed nonlinearity. We used the deduced stochastic model structure as a basis for evaluating the dynamic properties of this system. The dynamics is characterized either by limit cycles or chaos (the latter with a strong semi-periodic component). Stochasticity is seen to play an important role in the determination of the periodicity. The ecological implications of these statistical and mathematical results are discussed.

**Keywords:** microtine population cycles; deterministic processes; stochastic processes; nonlinear dynamics; dynamic stability analysis; continuous TAR models

## 1. INTRODUCTION

Periodic population cycles in small rodents and other terrestrial vertebrates of the north have preoccupied ecologists since Elton (1924, 1942) (cf. Cockburn 1988; Stenseth & Ims 1993a,b; Stenseth 1995; Stenseth *et al.* 1998a,b). Recently, much attention has been given to the presumed nonlinear nature of ecological interactions generating periodic fluctuations (e.g. Turchin 1993, 1995; Falck *et al.* 1995a,b; Framstad *et al.* 1997). Researchers have considered these fluctuations to represent limit cycles (May 1972; Stenseth 1977, 1985; Framstad *et al.* 1997), deterministic chaos (Turchin 1993; Hanski *et al.* 1993; Ellner & Turchin 1995; Turchin & Hanski 1997), or damped oscillations being sustained by environmental stochasticity (Stenseth *et al.* 1996a) with seasonality as a potentially important factor (Stenseth *et al.* 1998a).

Here we report on the population dynamic properties of statistical models resulting from nonlinear analysis of time-series of annual population growth rates of Norwegian lemmings (*Lemmus lemmus* (L.)). As an integral part of our analysis we consider the effect of stochastic resonance in nonlinear models (e.g. Rand & Wilson 1991).

## 2. THE DATA

Norwegian lemmings were studied on two permanent 1 ha grids (labelled M and H), 2.3 km apart, in the alpine zone (ca. 1250 m above sea level) at a mountain site at Finse, south Norway (60°36' N 7°30' E; Framstad *et al.* 1993a,b, 1997, their fig. 1a). The vegetation of the trapping grids is characterized by various mixes of dwarf shrubs, herbs, grasses, sedges, lichens, and mosses, with moderately high productivity on grid H and intermediate productivity on grid M. The climate is alpine (Østbye *et al.* 1975; Wielgolaski 1997a,b) with a short (2.5–3.5 months) and cool growing season (mean July temperature +8.0 °C), heavy snow cover in winter, and mean annual temperature of –2.1 °C (1961–1990; Aune 1993).

Since 1970, lemmings have been captured by kill-trapping twice a year (late June/early July, and in late August/early September, corresponding phenologically to spring and autumn, respectively). We have used regularly 1200 trap-nights (the number of traps multiplied by the number of nights they have been active) per grid and trapping session (with some reduction in trap numbers due to partial snow cover during some springs). We employ the number of captures per 100 trap-nights as our abundance index. For additional details about the trapping scheme and grids see Framstad *et al.* (1997). Between 1970 and 1995 a total of 3114 lemmings were caught on these two grids.

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As is common practice (cf. Henttonen *et al.* 1985; Stenseth & Ims 1993c), we restricted our analysis to the autumn data. In our case, this is essential due to the generally low density of lemmings in spring and the high number of zeros in the captures. Nevertheless, a similar but less pronounced pattern emerges from the spring samples (Framstad *et al.* 1997). In either case, a clear periodicity is observed and spring and autumn series are highly correlated.

### 3. AUTOREGRESSIVE MODELLING

#### (a) *Preamble*

Both the original and the log-transformed abundances were highly skewed (with a surplus of low values; Framstad *et al.* 1997). Following Framstad *et al.* (1997), we investigated the structure of the population growth rates  $r_t \equiv \ln(N_t/N_{t-1}) = \ln(N_t) - \ln(N_{t-1}) = n_t - n_{t-1}$  (where  $N_t$  and  $n_t$  are the non-transformed and log-transformed abundances, respectively). Due to the presence of zeros in the abundance data, a constant of 0.08 (equivalent to the capture of a single individual during a full trapping session) was added to each observation prior to log-transformation (see §4 for comments on the effect of adding constants of different magnitude). The analysed time-series (in  $r_t$ ) are depicted together with their spectral densities in figure 1. The growth rates (in  $r_t$ ) are assumed to be stationary (i.e. no trend), which seems reasonable by reference to the time-series plots in figure 1. The  $r_t$  series for both grids are characterized by a period of 3.4 years. For the purpose of analysis growth rates ( $r_t$ ) were standardized to mean zero and a standard deviation (s.d.) of one. (The original  $r_t$  series had means and s.d.s, respectively, of  $-0.162$  and  $3.297$  for grid H and  $-0.151$  and  $3.406$  for grid M. Notice that these (negative) means are not statistically different from zero.)

Using both the test for threshold nonlinearity (Chan & Tong 1990; Tong 1990) and the non-parametric test based on conditional means (Hjellvik & Tjøstheim 1995), Framstad *et al.* (1997) rejected the hypothesis of linearity at the 5% level for the  $r_t$  series from both grids.

The order of the process corresponds to the number of lags included in the model. Order determination by cross-validation (Cheng & Tong 1992) indicated that the optimal order of the  $r_t$  series was one for grid M and two for grid H. However, for either grid both orders one and two were quite competitive. We thus chose order one to be the overall best estimate. This is also in reasonable agreement with the conclusion of Framstad *et al.* (1997).

All statistical analyses reported in this paper were done using built-in and user-defined functions in *S-plus* (Venables & Ripley 1994).

#### (b) *Nonlinearity in periodic fluctuations of microtine rodents*

Whenever linearity is rejected, alternative nonlinear models must be specified. There are several ways of dealing with observed nonlinearity in ecology (May 1986; see also Tong 1990, 1995; Tjøstheim 1994). Part of the nonlinearity may be dealt with by expressing the net growth rates as functions of log-transformed abundances (Gompertz 1825). Such log-transformation is also appropriate in modelling population dynamics due to the

multiplicative nature of such population dynamic processes (Williamson 1972; Stenseth *et al.* 1996b). Moreover, the log-transformation stabilizes the variance (Sen & Srivastava 1990; Stenseth *et al.* 1996a,b).

Since the performance of individuals in the population may be qualitatively different during the pre-peak phase compared with the post-peak phase (Krebs 1978, 1996; Mihok & Boonstra 1992), a threshold approach (cf. Tong 1995) may be applicable (see also Framstad *et al.* 1997). Therefore, here we employ threshold autoregressive statistical models (TAR models; originally introduced by Tong (1978)).

#### (c) *Continuous TAR modelling*

Framstad *et al.* (1997) used a non-continuous threshold model (a self-exciting threshold autoregression model (SETAR), which is a piece-wise linear autoregressive model; see, for example, Tong (1983, 1990)). A non-continuous formulation may be supported if the threshold lies in a region of the state space for which there are few observations. However, many population models assume continuous rate functions (e.g. Edelstein-Keshet 1987; Stenseth & Chan 1998). We therefore extend the study of Framstad *et al.* (1997) by using a new statistical approach, continuous TAR models (Chan & Tsay 1998). Continuous TAR models are additive models (Hastie & Tibshirani 1990) and are thus special cases of multivariate adaptive regression splines (Friedman 1991; Lewis & Stevens 1991). From a statistical point of view, the continuous TAR model 'enjoys' the property that under suitable conditions estimators, including the thresholds, are asymptotically normal so that standard statistical techniques on confidence intervals and hypothesis testing are applicable. The SETAR model, however, provides more flexibility in fitting data, but requires greater skill in model identification. The analyses based on the two different statistical models provide similar conclusions and interpretations, thereby suggesting the generality of the conclusions.

Our basic model formulation is a continuous TAR(2;1,1) including a lower and an upper regime (see equations (1) below). (Note that the notation SETAR( $m$ ;  $p_1$ ;  $p_2$ , . . . ,  $p_m$ ) stands for a SETAR model with  $m$  regimes and the order of the  $j$ th regime equals  $p_j$ . The notation for a continuous TAR( $m$ ;  $p_1$ ;  $p_2$ , . . . ,  $p_m$ ) has a similar meaning for the continuous TAR models.)

$$r_t = a + \begin{cases} c(r_{t-1} - \theta) + \varepsilon_{(-),t} & \text{if } (r_{t-1} - \theta) \leq 0 \\ k(r_{t-1} - \theta) + \varepsilon_{(+),t} & \text{if } (r_{t-1} - \theta) > 0, \end{cases} \quad (1)$$

where  $a$  is a fixed parameter common to both regimes, and  $c$  and  $k$  are parameters referring to the lower and upper regimes, respectively;  $\theta$  is a threshold parameter separating the two regimes. Stochasticity (or dynamic noise),  $\varepsilon_{(\cdot),t}$ , is introduced as a sequence of independent random variables with mean zero and fixed variance,  $\sigma_{(\cdot)}^2$ . Statistically speaking, piece-wise linear autoregressive models are almost as easy to fit as linear autoregressive models, and the statistical properties of the sample estimates of unknown parameters are quite well developed (Tong 1990; Chan & Tsay 1998).

There are several advantages of a continuous TAR model over Framstad *et al.*'s (1997) SETAR model: (i) the

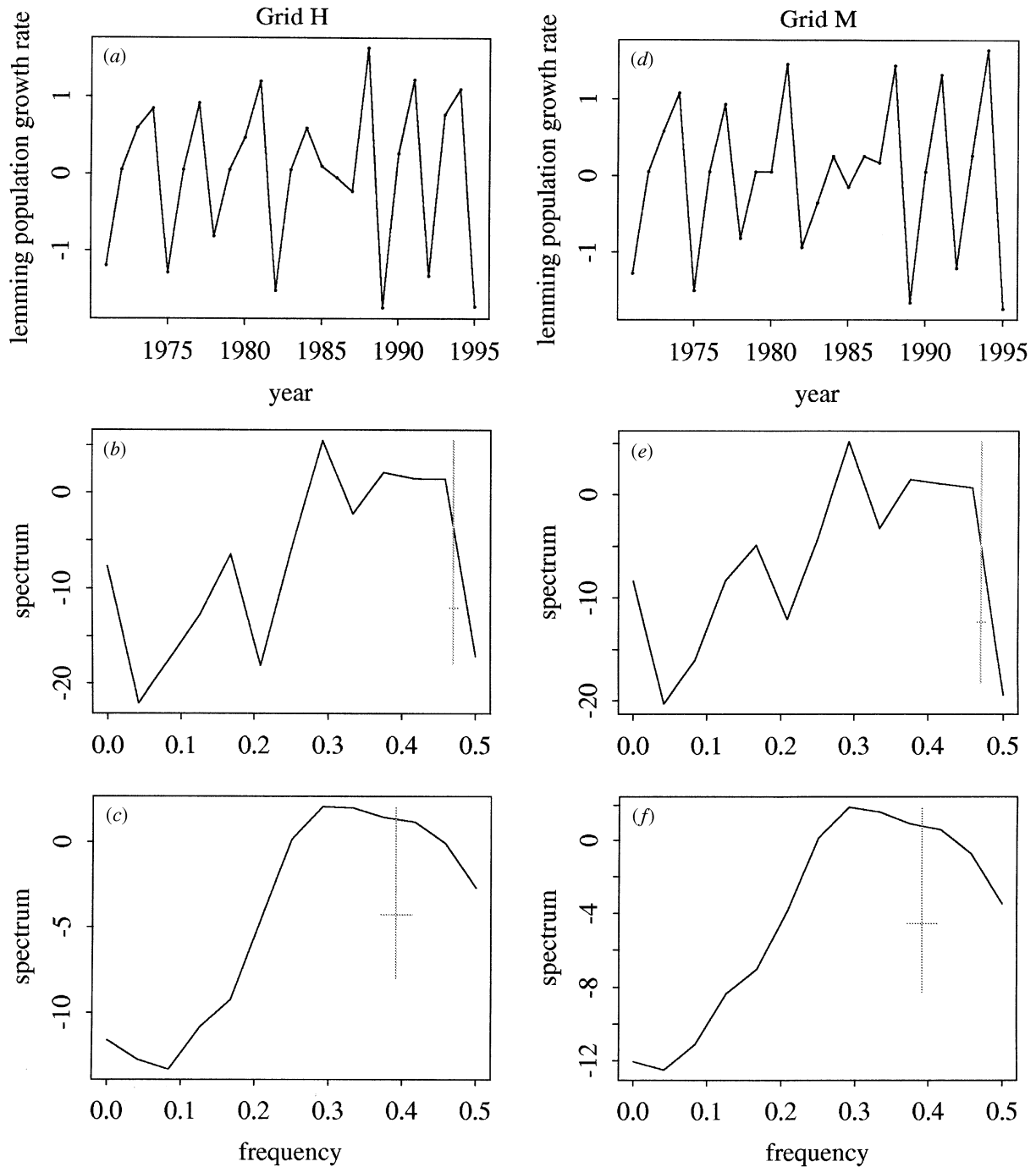


Figure 1. The time-series studied. (a) and (d) depict the two time-series (grids H and M, respectively) of yearly growth rates ( $r_t \equiv \ln(N_t/N_{t-1}) = \ln(N_t) - \ln(N_{t-1}) = n_t - n_{t-1}$ , standardized to mean zero and standard deviation one; see main text for further definitions). The raw periodograms (on the scale of  $10 \log_{10}$  where the unit is decibels; Venables & Ripley 1994, p. 357) for the two (mean-deleted) series are given in figures (b) and (e); used bandwidth is equal to 0.012, and the 95% confidence intervals of the spectrum values (in decibels) for both grids H and M are obtained by shifting the interval  $(-5.88, 17.57)$  by the corresponding periodogram estimates. The smoothed periodograms (again on the scale of  $10 \log$  where the unit is decibels) for the two series are given in figures (c) and (f); used bandwidth is 0.043, and the 95% confidence intervals of the spectrum values (in decibels) for both grids H and M are obtained by shifting the interval  $(-3.69, 6.46)$  by the corresponding periodogram estimates. The smoothing is done using the *S-plus* function `spectrum` with the span of the modified Daniel window specified as in `c(3,3)` (for details, see Venables & Ripley (1994), ch. 14; Bloomfield (1976), pp. 173–176). That is, the (log-) smoothed periodogram is obtained by smoothing the (log-) raw periodogram values using a moving average scheme with weights 1,4,6,4,1. The width of the centre mark on the 95% confidence interval indicator indicates the bandwidth. The smoothed spectra of the two grids are similar in shape, although the peak of grid M is higher; hence the cyclical structure in grid M is more pronounced. This serves as another indicator of the common dynamics enjoyed by the two processes (cf. formal tests for common dynamics reported in §4).

Table 1. *Parameter estimates for the threshold autoregressive models for Norwegian lemmings (Lemmus lemmus) at Finse, Hardangervidda, south Norway*

(Model fitting is done by the method of conditional least squares. The analysis of the SETAR model in (b) is redone for this paper, but the results are consistent with Framstad *et al.* (1997). Numbers in parentheses are standard errors for the given estimates. Number of years in the various regimes represents the number of observations falling in the respective regimes.)

(a) Analysis of the continuous TAR (2;1,1)-model (see the model given by equations (1))

population	$\theta$	$a$	$c$	$k$	number of years		RMS		AIC
					lower regime	upper regime	$\sigma_{(1)}^2$	$\sigma_{(2)}^2$	
grid H	0.46 (0.14)	0.76 (0.22)	0.29 (0.14)	-2.72 (0.53)	14	10	0.23	0.41	-21.15
grid M	0.18 (0.20)	0.86 (0.18)	0.58 (0.16)	-1.83 (0.38)	14	10	0.17	0.37	-26.34
pooled <sup>a</sup> estimate	0.43 (0.12)	0.81 (0.15)	0.38 (0.11)	-2.44 (0.34)	31	17	0.26	0.37	-51.15

(b) Analysis of the SETAR (2;0,1)-model (see the model given by equation (2))

population	$\theta$	$a_{(-)}$	$a_{(+)}$	$k$	number of years		RMS		AIC
					lower regime	upper regime	$\sigma_{(1)}^2$	$\sigma_{(2)}^2$	
grid H	0.10	0.40 (0.14)	2.04 (0.52)	-2.74 (0.54)	13	11	0.24	0.38	-21.27
grid M	0.05	0.20 (0.10)	1.37 (0.27)	-1.98 (0.29)	11	13	0.10	0.31	-32.39
pooled <sup>a</sup> estimate	0.25	0.40 (0.10)	1.96 (0.35)	-2.53 (0.33)	29	19	0.28	0.33	-49.98

<sup>a</sup>Pooled estimates were derived by minimizing the combined conditional least squares objective function; tests of null hypotheses of common dynamics (continuous TAR) and common parameters (SETAR) could not be rejected.

continuous TAR model has a built-in continuous conditional mean function which may be appropriate from ecological considerations; and (ii) statistical inference of the continuous TAR model may be tested via more or less classical techniques. The continuous TAR model provides less flexibility compared to the SETAR models, however. If the true model is a continuous TAR model (or an appropriate approximation, as is the case for the Maynard Smith & Slatkin (1973) model; see also Stenseth & Chan (1998)), then the SETAR fit and the continuous TAR fit must be similar. The converse is not true, however. The similarity of the fitted models (see § 4) suggests that the continuity assumption is appropriate in our case.

#### 4. STATISTICAL RESULTS

The statistical analysis indicates that a continuous threshold model of order one provides a better fit than a linear autoregressive model (as guided by the Akaike information (AIC) criterion (Tong 1990), under which  $AIC = -2 \ln(\text{maximum likelihood}) + 2(\text{number of parameters})$ , and where minimum values indicate best fit: continuous TAR(2;1,1)  $AIC = -21.15$  versus  $AR(2)$   $AIC = -17.10$  for grid H; and continuous TAR(2;1,1)  $AIC = -26.34$  versus  $AR(2)$   $AIC = -13.34$  for grid M). This is consistent with the nonlinear structure of the data (see § 3). A continuous TAR model of order two with the threshold in lag one does, however, outperform our

accepted model for grid H (TAR(2;2,2)  $AIC = -24.20$  versus TAR(2;1,1)  $AIC = -21.15$ ). As the difference in fit of models of order one and two is quite small, we suggest that the more parsimonious continuous TAR(2;1,1) model is appropriate. These conclusions are supported by cross-validation (see § 3). The sample autocorrelation function of the residuals reveals no further structure; hence, the TAR structure of the data seems acceptable. We therefore focus on a continuous TAR(2;1,1) model in the further analysis of the  $r_t$  series for lemmings.

The estimated continuous TAR(2;1,1) models for the two grids (H and M) are summarized in table 1a. Residual variances, the error terms  $\sigma_{(i)}^2$ , for grid H are larger than those for grid M. For both grids the error terms are larger for the upper regime corresponding to the post-peak phase (see below). Observing larger error terms during the post-peak phase may not be surprising since several factors might precipitate the crash.

We have studied the robustness of the continuous TAR model with different constants added to the original lemming data before converting them to the standardized lemming growth rates. We have used these additive constants: 0.01, 0.04, 0.08 (the 'standard'), 0.16, 0.32 and 0.48. By and large, the estimates are fairly robust with respect to changes in this constant. The estimate of the parameter  $k$  for grid H is the only exception in that it has larger changes with changes in this constant. However, this parameter also has a somewhat larger standard error. Our overall assessment is that the reported results and

conclusions are not critically dependent on the choice of the additive constant.

We have tested for identical parameters of the continuous TAR models for the two grids (the s.d.s excluded) and found no reason to reject the hypothesis of a common model structure ( $\chi^2 = 4.74$ ; 4 d.f.,  $p=0.32$ ). A comparable test of common structure (excluding the thresholds) for the SETAR models for the two grids gave similar results ( $\chi^2 = 2.84$ ; 3 d.f.,  $p=0.5$ ). The latter test should be interpreted with caution as the reported  $p$  value is correct only if the dynamics is discontinuous at the threshold (Chan & Tsay 1998). Pooled estimates are given in table 1. In the case of continuous TAR models with homogeneous Gaussian noise, the above test for common model structure is asymptotically equivalent to the likelihood ratio test (see Chan *et al.* (1998) for relevant discussions). Hence, these tests for common model structure should be reasonably powerful. Further studies are, however, needed to study their finite-sample behaviour.

Based on the AIC values, it appears that the continuous TAR model and the general SETAR model (equation (2) below) fit the  $r_t$  series from grid H almost equally well. The SETAR model outperforms the continuous TAR model for grid M, but the main gain seems to come from the lower regime. For the pooled data, the continuous TAR model outperforms the SETAR model. Hence, the continuous TAR model for the  $r_t$  series is quite competitive compared with the SETAR model.

## 5. THE DYNAMICS OF THE THRESHOLD MODELS

The class of continuous threshold models used in this paper is known to be rich in dynamic behaviour, ranging from limit points via limit cycles to chaos (Lim 1992*a-c*). Here we explore the model structure we found appropriate for the lemmings at Finse. We also evaluate the dynamic behaviour of the SETAR type of model originally reported by Framstad *et al.* (1997). Such dynamic analysis is usually done on *a priori* models not directly based on empirical data. The value of the following analysis is that the basic model is deduced on the basis of observed population dynamics changes. As part of our analysis, we investigate the effect of stochasticity.

### (a) *The original SETAR model*

Framstad *et al.* (1997) found the following non-continuous TAR model:

$$r_t = \begin{cases} a_{(-)} + \varepsilon_{(-),t} & \text{if } (r_{t-1} - \theta) \leq 0 \\ a_{(+)} + k r_{t-1} + \varepsilon_{(+),t} & \text{if } (r_{t-1} - \theta) > 0, \end{cases} \quad (2)$$

where the parameter estimates are given in table 1*b*.

The model given by equations (2) is depicted in figure 2*a*; the skeleton (the autoregressive model with stochastic dynamic noise suppressed; Tong (1990)) is characterized by a clear limit cycle (Framstad *et al.* 1997). Figure 2*b* summarizes the full description of the dynamic properties of this model. Superimposed on the parameter space given in figure 2*b* are the point-estimates together with their combined 95% confidence envelopes. As can be seen, the point-estimates for both grids fall within the three-period region of the parameter space. The

confidence region for grid H is wider than that for grid M, but both cover a wide variety of dynamic behaviour.

### (b) *The continuous TAR model*

Figure 3 summarizes the dynamic behaviour of the family of models corresponding to the model defined by equations (1). Figure 3*a* illustrates the model as such. Figure 3*b* shows the dynamic behaviour of the model. This diagram summarizes the results of a complete stability analysis of continuous TAR models. Figures 3*c* and 3*d* show the dominant period for various parts of the parameter space, both for the deterministic case (the skeleton), and for the stochastic model (the skeleton plus dynamic noise; see equations (1)).

As can be seen from figure 3*b*, the point-estimates for grid M fall marginally within the region with chaotic dynamics, whereas the point-estimates for grid H fall within the region with clear periodic oscillations. For both grids, a substantial part of the confidence region falls within the two-period region as well as within the chaotic region; the confidence region for grid H also falls within the three-period region.

Adding stochastic dynamic noise (figures 3*c-d*), we obtain a somewhat different pattern, which is easier to relate to the observed dynamics. Depending on the level of noise, a period of three to four years for grid M is entirely plausible. However, for grid H a somewhat shorter period is to be expected, as judged by the analysis of the skeleton. The periods for the TAR models are estimated to be 2.90 and 3.57 for grids H and M, respectively. The skeleton for the pooled TAR model has a limit cycle with period 2.00.

While the point-estimates of the relevant parameters fall marginally into the chaotic region, there is always a strong periodic component in the predicted dynamics. Under the influence of stochasticity, there is still a clear periodicity of three to four years, higher than the deterministic case, but within the range of observed periodicities in the data. The estimated residual variance ( $\sigma_{(\cdot)}^2$ ) is around 0.2 to 0.4 (table 1*a*). This suggests that the dominating periods illustrated in the lower-left diagrams of figures 3*c,d* apply (i.e. the panels with  $\sigma = 0.5$ ).

The impact of stochastic dynamic noise on the geometry of the attractors of the skeleton is in itself interesting. This was discussed by Takens (1994), as recorded in the discussions of Tong (1995), and needs further attention beyond the present paper. Here we only provide some preliminary reflections.

When  $k' (= -k) = 0$ , a flat spectrum occurs (all periods between two and  $+\infty$  are present in equal strength). As  $k'$  increases to one, more periods in the vicinity of two are introduced. Such periods cannot be observed in a purely deterministic system and are a result of what is called 'stochastic resonance' (cf. Rand & Wilson 1991; Dykman *et al.* 1993; Nicholis 1993; Nicholis *et al.* 1993; Wiesenfeld & Moss 1995).

Outside the fixed-point region of the parameter space, the 'shadowing lemma' prevents other periods than the deterministic ones from dominating as long as the amount of added noise remains small. (The shadowing lemma, roughly speaking, states that for a well-behaved (i.e. hyperbolic) dynamical system there exists an exact trajectory of the system without noise which will be arbitrarily

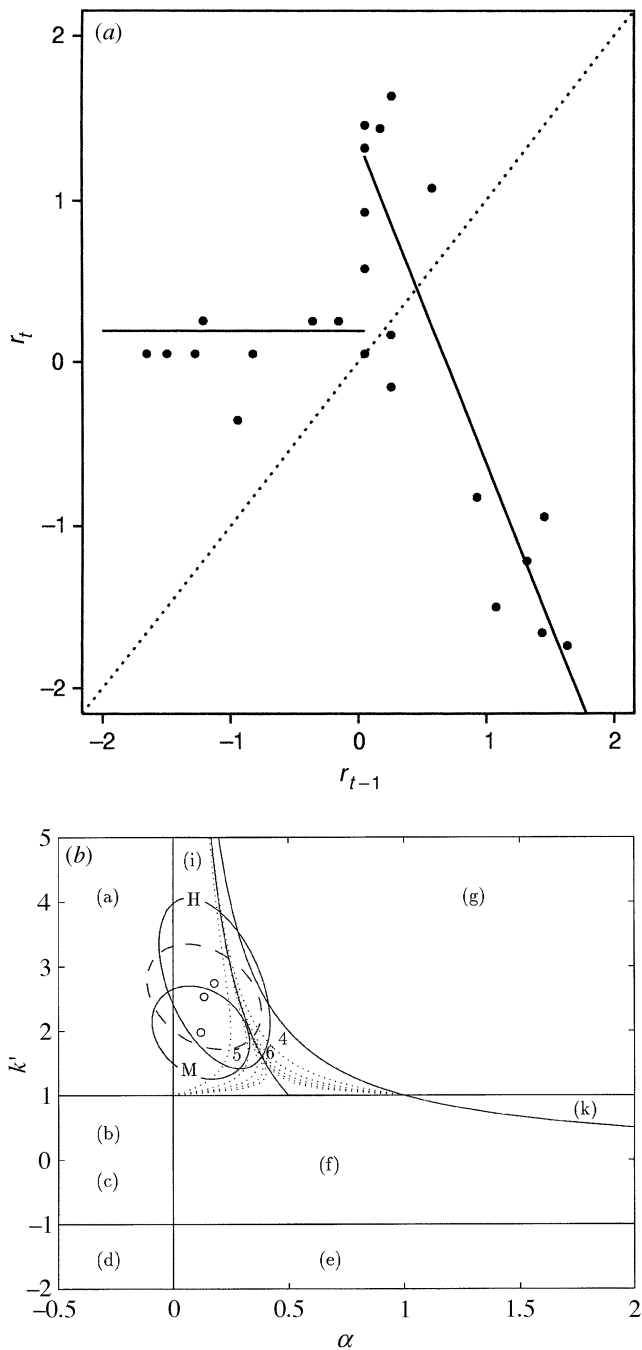


Figure 2. Mathematical analysis of the Framstad *et al.* (1997) model for the parameter space defined by the  $\alpha$  and  $k'$  parameters, where  $\alpha = (a_{(-)} - \theta) / (a_{(+)} - \theta - k'\theta)$  if  $(a_{(+)} - \theta - k'\theta) \neq 0$  and  $k' = -k$  (cf. equation (2), table 1b). (a) depicts the model for parameters  $\alpha = 0.5$  and  $k' = 3$  (roughly corresponding to the estimates for grid H): the dots show the data points; (b) shows the results of the analysis. Within the parameter space, the 95% confidence region corresponding to the estimates for grid H, grid M and pooled variables (broken curves) are represented as ellipses, with the respective point-estimates indicated by open circles. The various regions in the parameter space are as follows: (a) The fixed point  $r_t = \alpha$  attracts all solutions; (b) and (c) two coexisting attracting fixed points; (d) the fixed point  $r_t = \alpha$  attracts some solutions whereas the rest tend to  $+\infty$ ; (e) all solutions tend to  $+\infty$ ; (f) the fixed point  $r_t = 1/(1 + k')$  attracts all solutions; (g) a globally attracting two-periodic solution exists (this solution bifurcates into a four-periodic solution as indicated by the number in the figure, and later to a six-periodic solution, etc.); (i) a globally attracting

close to an observed trajectory of the system, now subject to noise, provided that the noise level is sufficiently small (Peitgen *et al.* 1992.) To distinguish this from the stochastic resonance defined above, we call this 'deterministic resonance'.

The fixed-point case indicates that stochastic resonance may also occur in the periodic and chaotic cases, although these resonances are less well understood, and as long as a small amount of noise is added in each case, they are hardly observable. In the two-period case we might, as an example, apply the stochastic resonance analysis for the fixed point case to the second iterate of the map equations (1), since it has two fixed points instead of a two-period orbit. As noise is added, it predicts high-periodic stochastic resonance as the two-period point emerges in the vicinity of  $k' = 1$ , and period four stochastic resonance as the two-period orbit disappears with increasing  $k'$ . The dominating period seems to increase somewhat as noise is added.

We should, however, not go too far in interpreting these results. Consider a linear stationary AR(2) model. Switching off the noise, we have a fixed point for the 'skeleton' and its non-normalized power density function is identically zero. However, switching the dynamic noise (however small) back on, the spectral peaks may be located anywhere between 0 and  $\pi$ , depending on the AR parameters. As a result, we should not expect to see the peak frequency as a smooth function of the noise level.

Nevertheless, since all ecological systems are influenced by a combination of deterministic and stochastic components, we suggest the interaction between these components to be an important topic of study within the field of ecology, a suggestion earlier made by Sugihara (1994) and recently emphasized by Grenfell *et al.* (1998). Indeed, with reference to the lemming population dynamics, we believe that our analysis suggests, for the first time so far as we are aware, that an important aspect of the underlying processes of the cycle may be found in this very interaction.

## 6. INTERPRETING THE MODELS BIOLOGICALLY

### (a) *Interpreting the two regimes*

Despite their structural differences, both TAR and SETAR models provide similar dynamics under the influence of stochasticity (resembling observed lemming dynamics). These models are based on our analysis of growth rates  $r_t$  and are formulated as piece-wise linear terms for two separate growth regimes (i.e.  $(r_{t-1} - \theta) \leq 0$  and  $(r_{t-1} - \theta) > 0$ ). As discussions on small rodent dynamics is usually framed in terms of increase, peak, crash and low density, we need to be explicit about the relationship between model regimes and phases of the three to four year population density cycles of lemmings. (Note here that  $r_t = n_t - n_{t-1}$  describes the population

(Continued) three-periodic solution exists (this solution bifurcates into a five-periodic solution, which bifurcates into a seven-periodic solution, etc.); and (k) a two-periodic attractor and an attracting fixed point solution coexist. Notice that the dynamic behaviour of the model of Framstad *et al.* (1997) is fully explored and completely described in (b).

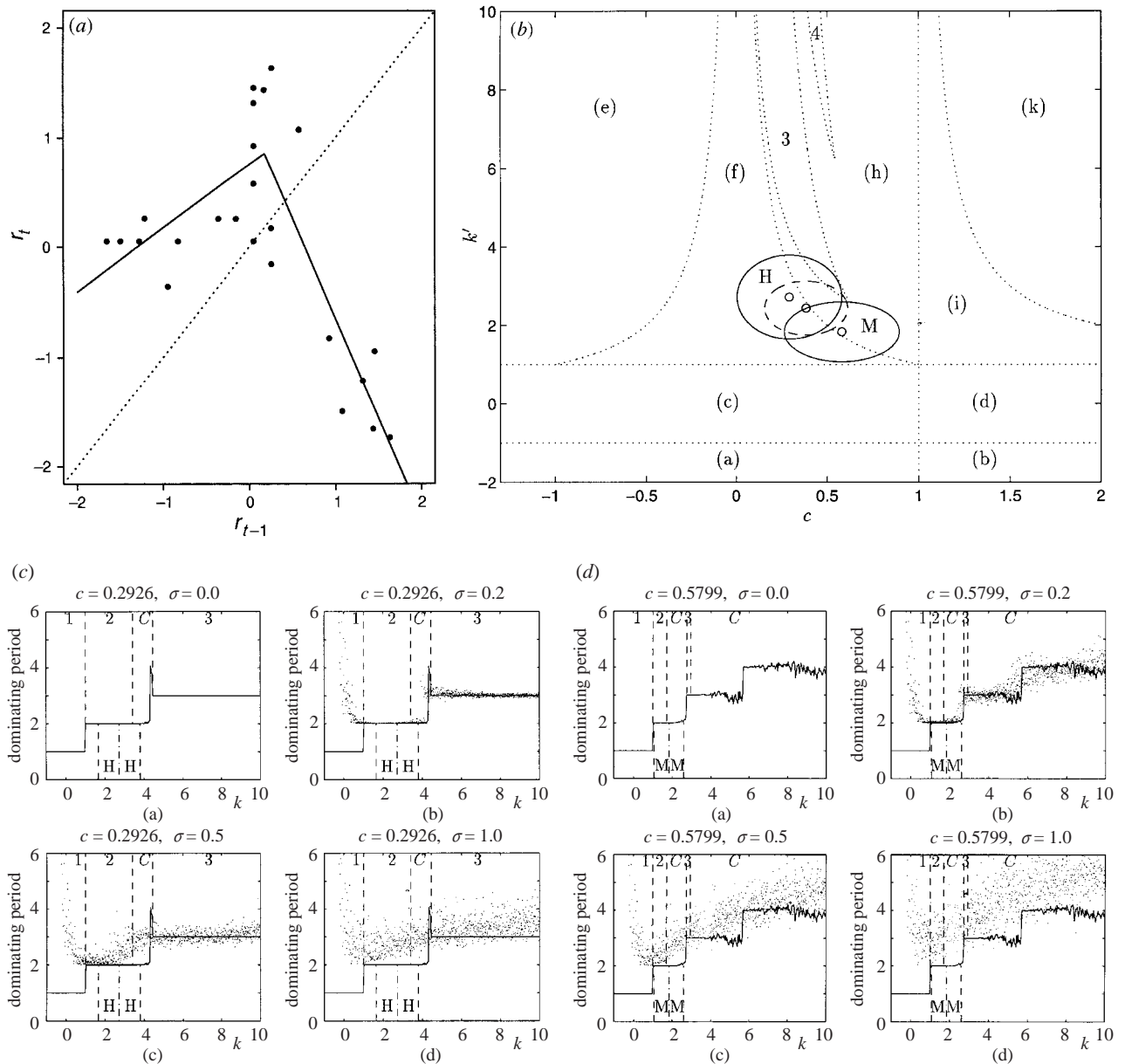


Figure 3. The population dynamics model corresponding to the continuous TAR model estimated in this paper is shown in (a); the dots show the data points. A change of coordinates removes the parameters  $a$  and  $\theta$  from the model (equations (1)) and its properties of population dynamics can be depicted in a  $(c, k')$  parameter space in (b). Within this parameter space, the 95% confidence regions corresponding to the estimates for grid H, grid M and pooled variables (broken curves) are represented by ellipses (the respective point-estimates are indicated by open circles). The various regions are as follows: (a) all solutions explode to  $+\infty$ ; (b) some solutions tend to the fixed point, the rest to  $-\infty$ ; (c) a globally stable fixed point; (d) some solutions tend to the fixed point, the rest to  $-\infty$ ; (e) unbounded oscillations; (f) at least locally stable two-periodic fluctuations exist (regions corresponding to three- and four-periodic locally stable solutions are denoted with three and four, respectively); (h) almost all solutions are attracted to a bounded chaotic solution; (i) almost all solutions starting within a special interval are attracted to a bounded and chaotic solution (solutions outside the interval tend to  $-\infty$ ); and (k) almost all solutions tend to  $-\infty$ . Figures (c) and (d) each depict the dominating period along increasing values of the  $k'$  parameter for the point-estimate of  $c$  corresponding to grid H (figure c) and to grid M (figure d), respectively. Within each panel, different levels of environmental stochasticity ( $\sigma$ ) is assumed (notice that the estimated levels correspond to  $\sigma = 0.5$ ; numbers within the diagrams along the top indicate the dominating period, whenever applicable, in the deterministic case (C indicates chaos); this dominating period is also shown as the curve within each diagram; the clouds with the dots correspond to the distribution of the found dominating periods for the corresponding system to which environmental (and dynamic) noise is added. As can be seen, the period in the stochastic case is generally higher than the corresponding period for the deterministic analogue. The diagrams shown in (c) and (d) present the results of Fourier analysis of the point-estimate of grid H, for various levels of noise ( $\sigma = 0.0, 0.2, 0.5, 1.0$ ). In the deterministic case ( $\sigma = 0.0$ ), grid H is represented by a stable period two-limit cycle (resonance indicated by a broken line), and the analysis of our paper says that as noise is added, more periods in the vicinity of four (resonance indicated by a dotted line) should be added the periods in the vicinity of  $\infty$ . As the level of noise is increased to  $\sigma = 2.0$  periods other than the deterministic period two are visible, but the strengths of these periods are not comparable to the deterministic period. A further increase in the noise level,  $\sigma = 0.5$ , the figure shows that other resonances than the deterministic ones become comparable to the deterministic resonance. However, the predicted stochastic resonance is not yet comparable with other not predicted resonances. When the level of noise is increased to  $\sigma = 1.0$ , neither the predicted stochastic resonance, nor the predicted deterministic resonance dominates the Fourier spectrum. The deterministic resonance is visible, but the stochasticity has destroyed the stochastic resonance before it became visible as a dominating period.

Table 2. *Distribution of years of population density cyclic phases versus model regimes*

(Actual autumn lemming catch data from Finse, south Norway, are employed. Years are classified as pre-peak, peak and post-peak, according to the general pattern of the density cycle and to the growth rate regime based on yearly density changes relative to the threshold of the continuous TAR model. The phase of low years of the occasional four-year cyclic periods has been deleted from the comparison. Figures in bold represent matching consistencies with the biological interpretation of the statistically deduced regimes presented in the main text.)

	regime	cyclic phase		
		pre-peak	peak	post-peak
grid H	lower	<b>7</b>	1	1
	upper	0	<b>5</b>	<b>7</b>
grid M	lower	<b>7</b>	<b>5</b>	1
	upper	0	1	<b>7</b>

changes occurring through the year from the previous autumn to the current autumn. The density changes leading up to the previous autumn (i.e.  $r_{t-1}$ ) determine the relevant model regime for  $r_t$ .

Focusing on the yearly density changes ( $r_t$ ), a three-year density cycle can be divided into the pre-peak, peak and post-peak years; population changes leading up to these years would be, respectively, low growth, rapid increase and crash. Due to the influence of population changes during the previous year ( $r_{t-1}$ ), the lower regime of the models ( $(r_{t-1} - \theta) \leq 0$ ) corresponds to the low growth leading up to the pre-peak year. Similarly, the upper regime ( $(r_{t-1} - \theta) > 0$ ) corresponds to the crash leading to the post-peak year. The rapid population increase leading up to the peak year will be associated with the upper regime if the growth rate leading up to the pre-peak year is greater than the threshold. Using actual observations from our two grids at Finse, we may classify years to growth regimes based on the estimated thresholds, and compare this to the general cyclic pattern of pre-peak, peak and post-peak years. For both grids, there is clear association between the lower regime and the pre-peak phase, and between the upper regime and the post-peak phase (cf. table 2). Years of peak density were primarily associated with the upper regime for grid H, but with the lower regime for grid M. This implies that the growth rate up to the pre-peak year (i.e.  $r_{t-1}$  with respect to the peak year) is substantially higher on grid H than on grid M, relative to the threshold for each grid (which is more than twice as large for grid H as for grid M).

The low, but positive, growth rate of the lower regime (leading up to the pre-peak year) is consistent with a recovery from food deterioration as well as from a predator-related suppression of the population after a crash. The rate of this recovery is indicated by the steepness of the transition between the two regimes. In the continuous TAR model (equations (1)), this is given by the parameter  $c$ ; the smaller it is, the faster and more pronounced is the transition between the two regimes. (Recall that  $r_{t-1} - \theta \leq 0$  in the lower regime.)

The population dynamics (figures 2 and 3), resulting from the derived skeletons, yield limit cycles, fixed points and chaotic regions, all of which are to some extent included within the confidence envelopes for the estimated parameter values of the models. Within the region of parameter space characterized by a limit cycle, the period, for the estimated parameters, is rather low (below four). Within the chaotic region there is also almost periodic oscillations, with generally low and rather stable period. Adding stochastic noise, the model periods become comparable to the observed periods for the series.

The threshold structure of our model is particularly convenient for focusing on phase shifts in the performances of the animals constituting the population during the different phases (Chitty 1960, 1967, 1996; Krebs 1978, 1993, 1996). The phase-dependence argument rests primarily on the existence of the threshold itself.

We expect the differences in performance of the animals from years corresponding to different phases, to be reflected by differences in demographic parameters. Acquiring good demographic data to characterize these regimes is problematic due to the numerical dominance of catches from the peak years and the reciprocal paucity of data from other years of the density cycle. Nevertheless, we have employed the threshold values of the continuous TAR models for the respective grids and classified the years based on observed changes in the autumn abundance of lemmings at Finse. For our data, the proportion of sexually mature males and females (classified by external characteristics) can then be compared to the years associated with the two regimes (only autumn catches are included; to avoid the effects of including juveniles, animals below a body weight of 30 g have been deleted). Based on these data, males tended to have a higher degree of sexual maturity during the upper regime (49% mature versus 35% mature during the lower regime; both grids combined,  $N=1237$ ,  $\chi^2$ -test,  $p < 0.0001$ ). Females on the other hand had a marginally higher frequency of sexual maturity during the lower regime (79%) than during the upper regime (70%) (both grids combined,  $N=1001$ ,  $\chi^2$ -test,  $p = 0.003$ ). A tentative interpretation is that males keep up their rate of sexual maturity well into the population crash. Females, on the other hand, tend to mature earlier during the slow population increase following the crash, but also reduce their sexual activity somewhat earlier during the peak and into the crash (but note that females tend to have a high sexual maturity rate, at least 70%, for both regimes). Females, in particular, may thus be seen to carry the population's transition from the crash to the increase. However, due to the dominance of data from a few peak years and the sensitivity to how these years are classified to either lower or upper regimes, considerable care is warranted in the interpretation of these results. In particular, note that due to differences in the classification of peak years to lower and upper regimes between the two grids (cf. table 2), the differences in maturity between the regimes are less pronounced for males on grid M and females on grid H. Ideally, we should base the comparison on characteristics of demographic performance of individuals in each year of the respective regimes. Regrettably, our own catch data are too skewed to make such a comparison meaningful. Certainly, such data are badly needed.



**(b) A possible scenario**

The upper regime of the statistical models may be seen as consistent with a mechanism based on predation (or other trophic interactions; see Framstad *et al.* 1997). The strength of the trophic interaction would then be characterized by the parameter  $k$ . Ecologically, population growth from the pre-peak year to the peak year may be possible because any large predator population has not yet had sufficient time to build up, while the crash following the peak year is easily interpreted as being mediated by heavy predation. The density-dependent structure of the model (equations (1)) is consistent with much of the current Fennoscandian literature on fluctuating microtine rodent populations focusing on predation as the key factor (Hanski *et al.* 1991, 1993; Hanski & Korpiimäki 1995; Stenseth *et al.* 1996b; Turchin & Hanski 1997; see also Hansson 1987). Our analysis suggests, however, that in our case predation may only be an important factor during the post-peak phase. Such an interaction between lemmings and predators, specializing on rodents, is important in a dynamic and interactive sense. It will account for the order-two structure of the model of the time-series on abundance (Framstad *et al.* 1997; cf. Stenseth *et al.* 1996b), this being compatible with an order one for the  $r_t$  series.

On the basis of this tentative interpretation, our derived threshold model may be considered consistent with the following 'combined phase- and density-dependent scenario'. This scenario is not new. However, we believe we are the first to base such a scenario on a consistent statistical pattern. Neither does our analysis exclude other scenarios. Nevertheless, the proposed scenario may be helpful when trying to integrate available data, as well as serving as a basis for suggesting further experimental studies.

- (i) The characteristics for the lower regime (i.e. the pre-peak phase) may be seen to correspond to the smaller constant term in the model of Framstad *et al.* (1997). Growth may be low for at least one of the following reasons (or a combination of them): food depletion and reduced quality (Batzli 1992; Agrell *et al.* 1995; Moen *et al.* 1993; Virtanen *et al.* 1997); or some form of maternal effect (Boonstra & Boag 1987; Mihok & Boonstra 1992; Boonstra 1994; Boonstra & Hochachka 1997). On the basis of currently available information, it is difficult to assess which of these is more likely (see also Boonstra *et al.* 1998).
- (ii) The transition between the lower regime and the upper regime coincides with the dynamic transition between the pre-peak and the post-peak phases. Such a transition may possibly be due to intrinsic or extrinsic processes. It would be intrinsic if some sort of demographic transition occurs (cf. Boonstra 1994; Tkadlec & Zejda 1998). It would also be intrinsic if (i) some genetic changes occur (Chitty 1960, 1967); or (ii) this transition occurs as a result of recovery of the vegetation (which might have been overgrazed during the peak phase, as may be the case in our system; see, for example, Moen *et al.* 1993). On the basis of currently available information, it is difficult to assess which of these is most likely.
- (iii) The nature of the crash for this model (equations (1)) may be seen to be due to some trophic interaction, such as predation by rodent specialist predators (Henttonen 1987; Henttonen *et al.* 1987; Erlinge *et al.* 1983, 1984; Erlinge 1987; Norrdahl 1995) or interactions with the food supply (Batzli 1992). Much current evidence favours the predation alternative (see, for example, Stenseth *et al.* 1996b).

Focusing only on predation (as is done in much of the current literature on microtine population ecology) excludes the consideration of potentially important dynamic interactions between lemmings (and other microtine rodents) and vegetation. Within our scenario, overgrazing of the vegetation might, however, play some role in explaining the syndrome of low maximal growth during the post-peak phase. Moen *et al.* (1993) did, for instance, observe that there is a strong impact of lemmings on the plants during the peak (see also Kalela *et al.* 1961, 1971; Henttonen & Järvinen 1981; Oksanen & Oksanen 1981; Oksanen 1993). Moen and co-workers showed, however, that the recovery of the plants is evident only immediately after the decline, especially amongst the mosses (which constitute a major part of the diet of lemmings; see, for example, Hansson 1969, 1985; Kalela & Koponen 1971; Tast 1991; Batzli 1993).

In summary, it thus seems that the pre-peak phase year may be due to destruction of the food supply by overgrazing during the preceding peak year. The transition from the lower regime to the upper regime may be due to a short-term lag in the recovery of the vegetation. The crash may be due to heavy predation by predators specializing on lemmings and voles. This would then be characterized as a multifactorial view of the rodent cycle, somewhat resembling the view of, for instance, Lidicker (1988, 1991). Our version is, however, testable through experimental manipulations (Gaines *et al.* 1991) involving, for instance, predator exclusion (during the post-peak phase of the lemming cycle) and food addition (during the initial part of the pre-peak phase of the cycle). On the basis of our analysis it seems particularly worthwhile to obtain a better grasp of the *combined* effects of dynamic trophic interactions and phase shifts of the individuals constituting the population. Furthermore, understanding why individuals seem to perform worse during the initial post-peak phase than during other parts of the cycle is certainly of critical importance. We expect that adding high-quality food would raise the growth rate of the lower regime, making the constant term higher and possibly the lag-one term different from zero (for the SETAR model) and flatter (for the continuous TAR model). Excluding predators would reduce the slope of the upper regime. Performing such experiments would be difficult. However, taking a comparative approach using different populations may indeed provide the required information.

We further need to decouple phase and density effects in a systematic design. A series of introduction experiments in which individuals from a given phase of the cycle are introduced into large enclosures at variable densities might indeed be rewarding. The resulting dynamics, corrected for the fence effect (Krebs *et al.* 1969; Krebs 1992), should allow us to partition the variability

in reproduction and mortality which is caused by density- and by phase-dependencies. Similar types of experiments have been done by, for instance, Ostfeld & Canham (1995) and Johannesen & Ims (1996) but on *Microtus* populations with no clear cyclic structure. Similar work is badly needed for lemmings: the classic cyclic vertebrate species of northern regions.

Finally, in order to understand the effect of statistical resonance we further need to perform such experiments under the influence of different levels of environmental stochasticity. For this purpose, a comparative approach seems preferable.

## 7. CONCLUSION

A basic philosophy of our work has been to use the best available and most appropriate statistical tools. Specifically, we use these statistical tools for two purposes: (i) to gain insights into some aspects of the biological process and (ii) to highlight areas where further biological experiments and field work may be necessary before a fuller understanding of the biological process is possible.

We are left with the conclusion that the Norwegian lemmings in the mountains of south Norway have density-dependent-dynamics (including both direct and delayed density-dependence) which is also phase-dependent. This supports our previous analysis (Framstad *et al.* 1997). Here we have extended that analysis in several respects. Most importantly, we have conducted ecological stability analyses of both the original model of Framstad *et al.* (1997) and the continuous TAR model derived here, emphasizing the interplay between deterministic and stochastic processes. Thus, we have coupled the derived model dynamics more directly to the observed lemming dynamics.

Seeing the lemming and microtine cycle as a combined phase- and density-dependent structure might indeed help us forward. Dramatically changing conditions for the animals constituting the population at any given time (in any particular phase of the cycle) may cause the proposed phase-dependent nonlinearity. We are convinced that an integrated approach like the one we have taken in this paper, using both statistical and mathematical modelling coupled with empirical studies, will be needed to unlock the long-lasting enigma of the lemming population cycle. At the conceptual level, there is substantial evidence for a combined hypothesis, where both trophic dynamic interactions and phase-shifts in the performance of the individuals may represent keys to unlock the lemming cycle. Finally, a major conclusion of this paper is that we also need to understand the interaction between environmental and nonlinear deterministic processes.

Support for the collection of data has been provided by the Research Council of Norway, the Nansen Endowment, the University of Oslo, the High Mountain Research Station of the University of Oslo and the University of Bergen at Finse, and the Norwegian Institute for Nature Research. We are particularly grateful to Eivind Østbye who initiated the studies of lemmings at Finse and whose efforts have been essential for the maintenance of the early part of the series. K.-S.C. has been funded by NSF grant DMS 9504798 and a faculty scholar

award from the University of Iowa. N.C.S. was funded by the Centre for Advanced Study of the Norwegian Academy of Science and Letters, and a strategic university grant from the National Science Council. H.T. has been funded by the CRCG of Hong Kong, the Engineering and Physical Science Research Council, UK (grant GR/L16385) and a European Community Human Mobility grant (no. ERB CHRX-CT-94-0693). The technical analysis underlying the results reported in figures 2 and 3 was done by Dr Törsten A. Lindström (who will in due course report details of this analysis). T. A. Lindström has also provided valuable input to the entire paper, in particular to §5. Ottar N. Bjørnstad, Rudy Boonstra, Mads C. Forchhammer, Charles J. Krebs, Eric Post and Nigel G. Yoccoz are thanked for valuable comments on an earlier version of this paper; four anonymous reviewers are thanked for their valuable input.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.