

# Limit cycles in Norwegian lemmings: tensions between phase-dependence and density-dependence

ERIK FRAMSTAD<sup>1</sup>, NILS C. STENSETH<sup>2\*</sup>, OTTAR N. BJØRNSTAD<sup>2</sup>  
AND WILHELM FALCK<sup>2</sup>

<sup>1</sup> Norwegian Institute for Nature Research (NINA), P.O. Box 736 Sentrum, N-0105 Oslo, Norway

<sup>2</sup> Division of Zoology, Department of Biology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway

## SUMMARY

Ever since Elton, the 3–5 year density cycles in lemmings (and other microtines) in Fennoscandia have troubled scientists. Explanations have involved intrinsic regulation and trophic interactions. We have analysed yearly changes in fall abundances for lemmings over 25 years from two local mountain sites in South Norway. These time series appear to have an underlying nonlinear structure of order two. Fitting a piece-wise linear threshold model of maximum order two, the most parsimonious model was, however, of first order for both series. The resulting dynamics from this model is a limit cycle. Reformulating the model in terms of abundances yields a model which combines (delayed) density-dependent effects and the influence of the cyclic phase. The delayed density-dependence of one part of the model is consistent with an effect of specialist predators during the peak and crash phases of the cycle, although other trophic interactions cannot be excluded.

## 1. INTRODUCTION

The 3–5 year density fluctuations in lemmings are well known to scientists and laymen alike (cf. Finerty 1980; Stenseth & Ims 1993*a*). In modern ecological research, these density cycles have troubled biologists since Elton's pioneering work (Elton 1924, 1942; see also Shelford 1943; Krebs 1964, 1993; Pitelka 1973; Pitelka & Batzli 1993; for reviews, see Stenseth & Ims 1993*a, b*). One dominating view has been that lemmings (and other microtines) are regulated by intrinsic factors (Chitty 1960; Krebs 1964, 1978; Charnov & Finerty 1980), in effect resulting in dynamics which depend on the population cyclic phase rather than the population density *per se* (hereafter referred to as 'phase-dependent dynamics').

Trophic interactions have also been suggested to play key roles in the generation and maintenance of microtine population cycles: Lack (1954) suggested that they resulted from interactions with the food supply (see, for example, Batzli (1992) for a recent review). More recently, several authors have argued that predation is the key factor (Hanski *et al.* 1991, 1993; Hanski & Korpimäki 1995; Norrdahl 1995; Norrdahl & Korpimäki 1995). May (1972) suggested, on the basis of available evidence, that trophic interactions could easily give rise to stable limit cycles. However, this has never been demonstrated empirically for microtines (cf. Gilbert 1984). The mere existence of nonlinearity has in fact been demonstrated

for only one microtine (*Ondatra zibethica*; Tong 1983) – otherwise it has only been assumed or concluded from theoretical models (e.g. May 1972; Hanski *et al.* 1993; Turchin 1993, 1995).

Here we show, by employing the threshold autoregressive models of Tong (1993), that Norwegian lemmings (*Lemmus lemmus*) exhibit nonlinear dynamics, that the dynamics are both phase- and density-dependent, and that they may adequately be described as a limit cycle. On the basis of these results we suggest that both intrinsic processes and a trophic interaction are essential in the generation of the lemming cycle.

## 2. THE SPECIES AND THE DATA

We have studied Norwegian lemmings (*Lemmus lemmus* (L.)) on two permanent 1 ha grids, 2.3 km apart, in the alpine zone (*ca.* 1250 m above sea level) at the mountain site of Finse in southern Norway (60° 35' N, 7° 30' E) (Framstad *et al.* 1993*a, b*) (figure 1). The vegetation of the trapping grids is considered to be of moderately high (grid H) and medium (grid M) productivity for this area, and is characterized by various mixes of dwarf shrubs, herbs, grasses, sedges, lichens, and mosses. The climate is alpine (Østbye *et al.* 1975) with a short (2.5–3.5 months), cool growing season (mean July temperature of +8.0 °C), with heavy snow cover in winter often exceeding 4 m in depth, and with a mean annual temperature of –2.1 °C (1961–1990; Aune 1993).

\* Corresponding author.

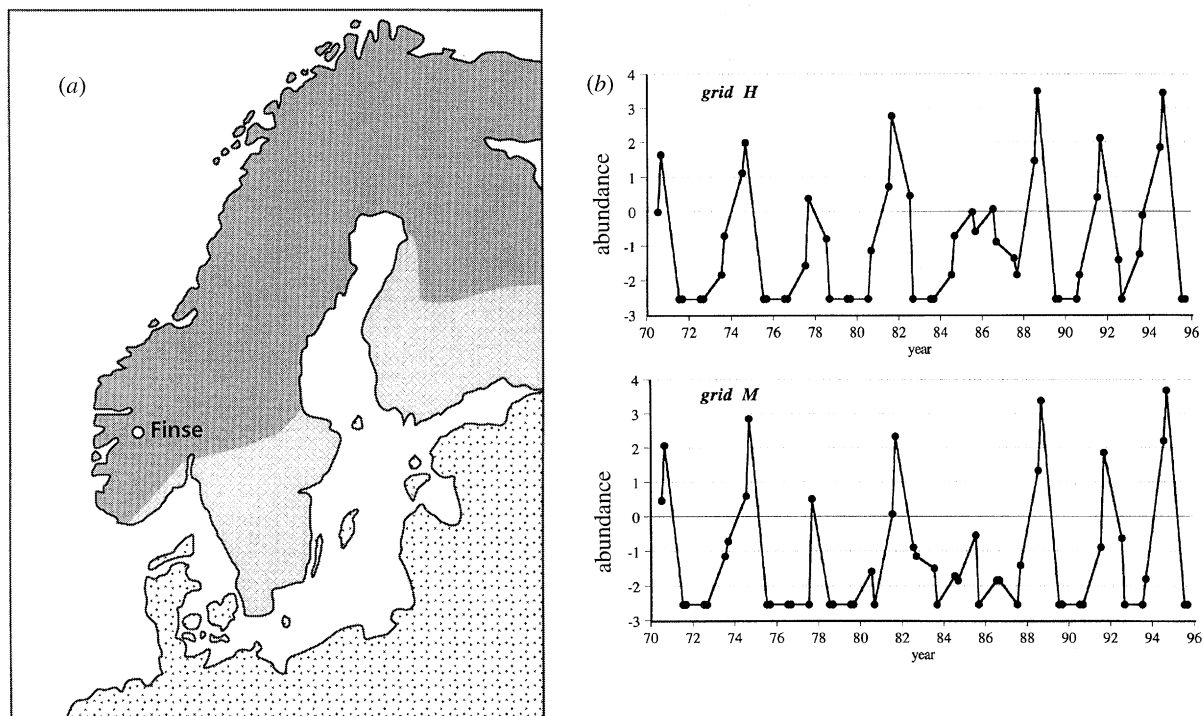


Figure 1. (a) Location of the study site at Finse, South Norway ( $60^{\circ}36' \text{ N}$ ,  $7^{\circ}30' \text{ E}$ ). The zone of strongly cyclic rodent population fluctuations in Fennoscandia is indicated by dark shading (redrawn from Hansson & Henttonen (1988)). (b) Time trajectories of the ln-transformed relative abundances (catch per 100 trap-nights+0.08) of Norwegian lemmings (*Lemmus lemmus* (L.)) on two trapping grids (H, M) for the period 1970–1995.

Lemmings were captured on these 1 ha grids by snap-trapping twice a year (end of June/beginning of July – termed spring; end of August/beginning of September – termed fall) from 1970 until present. We have regularly used 1200 trap-nights per grid and trapping session, but with some reduction in trap numbers due to partial snow cover during some spring sessions. We employ the number of captures per 100 trap-nights as a standardized abundance index. Since 1970, a total of 3114 lemmings have been caught on these two grids. Besides lemmings we have caught: *Microtus oeconomus* (16.4% of total catches on grids H and M combined), *M. agrestis* (2.5%), *Clethrionomys glareolus* (2.1%), *C. rufocanus* (1.0%), and *Sorex araneus* (1.7%). Hence, lemmings tend to dominate the small mammal community; however, *M. oeconomus* was numerically dominant on grid H during the 1970s (Framstad *et al.* 1993a).

The relative abundances of lemmings as revealed in the fall catches were frequently very high, and resulted in pronounced and rather consistent regular fluctuations (figure 1). The overall lower abundances in the spring result in less pronounced fluctuations, which presumably are more sensitive to random sampling variation. There is considerable covariation in the fluctuation patterns of the spring and fall time series for both grids (figure 1). However, the less consistent fluctuations of the spring series did not permit consistent analyses of these series. Hence, only the fall time series have been used for further analysis. Focusing on fall abundances is also consistent with recommendations by Henttonen *et al.* (1985).

The consistent fluctuation pattern and the numerical dominance of lemmings at our study site at Finse indicate that this alpine area is part of the core range of Norwegian lemmings. Other long-term Fennoscandian small rodent studies which include lemmings are placed in the low alpine, subalpine birch or taiga zones. These sites appear to be more marginal within the lemming range, with less regular population fluctuations of lemmings (e.g. Kalela 1971; Henttonen & Järvinen 1981; Henttonen *et al.* 1987; Oksanen & Oksanen 1992; Henttonen & Kaikusalo 1993). Our analysis may therefore not be directly applicable to other available long-term time series for Norwegian lemmings.

The rapid increase to high abundance in lemmings (figure 1) is possible because of their high reproductive potential. A female may have an average of six (1–12) young in a litter, pregnancy is 21 d and age of maturation in the field is typically 5 weeks (reviewed in Stenseth & Ims 1993c). Sex ratio at birth is approximately 50:50 (A. Semb-Johansson unpublished data). Post-partum oestrus is common (Semb-Johansson *et al.* 1993), so that a female may produce three or more litters during the summer. A common feature appears to be frequent subnivean winter reproduction (E. Framstad *et al.* unpublished data; see also Hansson 1984). Due to the length of the winter, subnivean winter reproduction may have more pronounced effects in the lemming species than in most other microtine species (cf. Kaikusalo & Tast 1984; Sittler 1995).

The predator community of the study area relevant

to small rodents consists primarily of red foxes (*Vulpes vulpes*), Arctic foxes (*Alopex lagopus*), stoats (*Mustela erminea*), weasels (*M. nivalis*), ravens (*Corvus corax*), rough-legged buzzards (*Buteo lagopus*), kestrels (*Falco tinnunculus*), and common gulls (*Larus canus*) (Østbye *et al.* 1975). Among these, stoats and weasels have been in focus in many studies of Fennoscandian rodents because they are considered to be specialist predators of microtines (Norrdahl 1995). That is, their demography is numerically and reproductively linked to the rodents (e.g. Hanski *et al.* 1991). Studies of the diet of birds of prey (Hagen 1952) indicate that lemmings are less favoured food items than other microtines; it is even suggested that lemmings are not very palatable (Taitt 1993). Hagen (1952) argued that this is perhaps the reason why lemmings are allowed to reach such extreme densities.

### 3. STATISTICAL MODELS AND TREATMENTS

Microtine population dynamics have at various stages been considered phase-dependent (e.g. Krebs 1978) and density-dependent (e.g. Hörnfeldt 1994; Bjørnstad *et al.* 1995). From a modelling perspective, density dependence is usually formulated as  $r_t = g(N_t, N_{t-1}, \dots, N_{t-k})$ , where  $N_t$  is the abundance at time  $t$ ,  $g(\cdot)$  is a general function for density dependence (e.g. Turchin & Millstein 1993), and  $r_t$  is the growth rate given by  $\ln(N_{t+1}/N_t)$ . A possible analogous phase-dependent model would be  $r_t = f(r_t, r_{t-1}, \dots, r_{t-k-1})$ . For certain specifications of  $g(\cdot)$  and  $f(\cdot)$  there will be a duality between the density-dependent and the phase-dependent models. For instance, a linear first-order phase-dependent model may be considered in terms of a second-order (delayed) density-dependent model (with constraints on the parameters).

A crucial issue is to select the functional form for  $f(\cdot)$  or  $g(\cdot)$ . Unless the data indicate otherwise, a log linear model for  $f(\cdot)$  may be advocated (e.g. Royama 1992; Hörnfeldt 1994; Bjørnstad *et al.* 1995). In such a situation, the statistical model will be identical to a standard linear autoregressive (Box-Jenkins) model – a model for which both the dynamic (e.g. Royama 1992) and statistical (e.g. Wei 1989) properties are well-known.

Several goodness-of-fit tests are necessary in order to find a suitable model. First, the data should adhere approximately to a symmetric homoscedastic distribution (e.g. a normal distribution). This amounts to finding a suitable scale – which is usually the log-scale for biological populations since population dynamics are multiplicative. Second, deviations from linearity on this transformed scale should be assessed. Various tests for nonlinearity in time series exist, but few have been properly investigated for the present small sample situation. The main problem is related to low power when data are scarce; one may end up retaining the null hypothesis of approximate linearity (on the log scale) when this is not true (i.e. a type II error). In the present analysis we employ two tests for nonlinearity: a test for threshold nonlinearity (Chan & Tong 1990;

Tong 1993) and a non-parametric test based on the conditional means (Hjellvik & Tjøstheim 1995).

Whenever approximate linearity is rejected, one is faced with the task of finding an alternative nonlinear model. The problem is that while there is only one form of linearity, nonlinearity may take an infinite number of different forms (e.g. Tong 1993; Tjøstheim 1994). The curse for ecological time series analysis is that flexible models are usually associated with a large number of free parameters that may consume the number of observations completely (Falck *et al.* 1995a). Below we focus on simple threshold autoregressive models (self-excitatory threshold autoregressive models – SETAR, that is, piece-wise linear autoregression (Tong 1983, 1993)). This model-structure has previously been fitted to some of the classical ecological time series (lynx, *Lynx canadensis*: Tong 1993; blowflies, *Lucilia cuprina*: Chan & Tong 1986; Tsay 1988; muskrat, *Ondatra zibethica*: Tong & Lim 1980).

Both the original and the log-transformed abundances in our series had very skewed distributions (with a surplus of low values). No simple transformation of the data appeared to stabilize the variance satisfactorily as required for the fitting of the series to time series models. Hence, we investigate the sequence of growth rates  $r_t \equiv \ln(N_{t+1}/N_t)$  (cf. Sugihara & May 1990). Such an analysis of growth rates represents a difference in abundances which also promotes stationarity of the series (Box & Jenkins 1976). Due to the presence of zeroes in the abundance data, a constant equal to 0.08 (equivalent to the capture of a single individual during a full trapping session) was added to each observation prior to log-transformation. Without loss of generality, growth rates were scaled (mean = 0, SD = 1) prior to analysis.

As indicated, we employ a piece-wise linear threshold autoregressive model in  $r_t$  with one threshold as an alternative to the log linear model. Denoting  $r_t$  as the growth rate at time  $t$  and  $d$  as the order (maximum lag), we may write this model as:

$$r_t = \begin{cases} a_{1,0} + a_{1,1}r_{t-1} + a_{1,2}r_{t-2} + \dots + a_{1,d}r_{t-d} + \epsilon_{1,t} \\ \quad \text{if } r_{t-1} = \ln(N_t/N_{t-1}) \leq \beta \\ a_{2,0} + a_{2,1}r_{t-1} + a_{2,2}r_{t-2} + \dots + a_{2,d}r_{t-d} + \epsilon_{2,t} \\ \quad \text{if } r_{t-1} = \ln(N_t/N_{t-1}) > \beta \end{cases} \quad (1)$$

where  $a_{i,0}, a_{i,1}, a_{i,2}, \dots, a_{i,d}$  correspond to the estimated parameters for the two regimes ( $i = 1, 2$ ) below and above the threshold ( $\beta$ ), and  $\{\epsilon_{i,t}\}$  is a sequence of independent, normally distributed, state-independent random variables with mean zero.

Once it has been determined if a linear or nonlinear model is more appropriate, the order must be determined. We have employed cross-validation using a non-parametric method (Cheng & Tong 1992) to determine the maximum order for further consideration. For comparison we have also calculated the cross-validation based on the linear autoregressive model (see Kohn & Ansley (1986) for ARIMA estimation with deleted observations). When fine-tuning the final model we use the AIC<sub>c</sub> (Hurvich & Tsai 1989; see also Tong 1993). See, for instance,

Royama (1992), Bjørnstad *et al.* (1995), and Stenseth (1995) for a discussion of the ecological significance of the order.

To investigate if the two segments of the piece-wise model are significantly different at the threshold, confidence intervals for the predicted values at this point were calculated using classical linear regression theory (e.g. Sen & Srivastava 1990, ch. 3). The pooled variance of the SETAR3 model was used as the variance for both regimes.

The analyses were carried out using S-plus for Windows version 3.2 (Statistical Sciences 1993) and SETAR3 (Tong 1993). The non-parametric order estimates and test for nonlinearity was calculated using a code compiled in Borland Pascal version 7.0 (Borland 1992) interfaced with S-plus.

#### 4. RESULTS

The null hypothesis of linearity was rejected at the 5% level for both series (grid H: non-parametric tests,  $p = 0.02$ ; threshold test,  $p < 0.01$ ; grid M: non-parametric tests,  $p < 0.01$ ; threshold test,  $p < 0.01$ ). Thus, the evidence against linearity is overwhelming.

Order estimation (figure 2) indicates that order two is appropriate. The optimum order of the linear model diverges from the non-parametric by indicating that order three and four are slightly better than two. This is likely to be a reflection of the nonlinearity of the underlying process (Royama 1992: ch. 2) and is the artefact of imposing linear constraints on a nonlinear process. From the nonparametric model it is clear that, if not two, the order is closer to one than three or four ( $CV_1 < CV_3 < CV_4$ ; see figure 2).

Following the order estimates (figure 2) we have used a piece-wise linear, one-threshold model of maximum order 2 ( $d$  in equation (1)). The most extensive second order, piece-wise linear threshold model to be applied to the two series (H, M) is therefore:

$$r_t = \begin{cases} a_{1,0} + a_{1,1}r_{t-1} + a_{1,2}r_{t-2} + \epsilon_{1,t} & \text{if } r_{t-1} = \ln(N_t/N_{t-1}) \leq \beta \\ a_{2,0} + a_{2,1}r_{t-1} + a_{2,2}r_{t-2} + \epsilon_{2,t} & \text{if } r_{t-1} = \ln(N_t/N_{t-1}) > \beta. \end{cases} \quad (2)$$

Thresholds were selected to give optimal models (as judged by  $AIC_c$ ). For both series the most parsimonious structure of the threshold autoregressive model was (table 1):

$$r_t = \begin{cases} a_{1,0} + \epsilon_{1,t} & \text{if } r_{t-1} = \ln(N_t/N_{t-1}) \leq \beta \\ a_{2,0} + a_{2,1}r_{t-1} + \epsilon_{2,t} & \text{if } r_{t-1} = \ln(N_t/N_{t-1}) > \beta. \end{cases} \quad (3)$$

Note that the lower regime is represented by a constant and that the upper regime includes one of the maximum of two lags (in  $r_t$ ). Plots and tests of residuals from the models for both fall series indicated that these were reasonably approximated by symmetrical noise (SETAR3; Tong 1993).

The estimated models and parameter values gave essentially the same result for both series. Based on

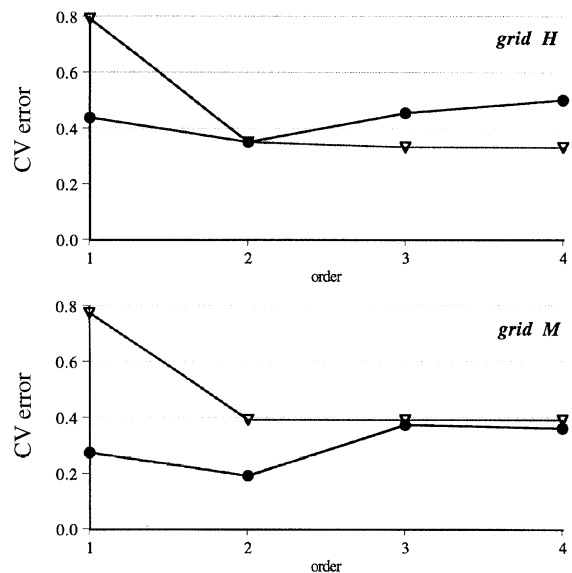


Figure 2. Order estimates for the time series of growth rates from grids H and M, based on both linear autoregressive (grey lines and open triangles) and non-parametric (solid lines and circles) models. Cross validation error (CV error) is plotted against model order.

inspection of the spectral density function (Wei 1990), a significant periodicity of 3.4 was found for both time series. Simulating the skeletons (equation (3) without noise) of the fitted models results in limit cycles of (fixed) period 3. The skeleton for the fitted model for the  $r_t$  series for grid H is shown in figure 3b. As can be seen from the 95% confidence intervals of the growth rates (table 1), for both grids the growth rate for the lower segment is significantly less than the maximum rate of the upper regime (cf. figure 3). The selected threshold values for the series were similar (table 1), suggesting some particular underlying biological process (below).

#### 5. DISCUSSION: COMBINING PHASE-DEPENDENT AND DENSITY-DEPENDENT DYNAMICS

Even though we have based the analysis on the growth rates ( $r_t$ ), the structure of the statistically deduced model shows clear similarities to linear autoregressive models obtained for log-abundance data of other rodent species (Bjørnstad *et al.* 1995). That is, equation (3) may be rewritten as

$$N_{t+1} = \begin{cases} N_t \exp[a_{1,0} + \epsilon_{1,t}] & \text{if } \ln(N_t/N_{t-1}) \leq \beta \\ N_t \exp[a_{2,0} + a_{2,1} \ln(N_t) - a_{2,1} \ln(N_{t-1}) + \epsilon_{2,t}] & \text{if } \ln(N_t/N_{t-1}) > \beta. \end{cases} \quad (4)$$

The two growth rate regimes relate to different phases of the cycle rather than to density levels. This model may therefore appropriately be referred to as a combined density-dependent and phase-dependent model, where the threshold  $\beta$  represents the phase-dependence, and the lagged regressions on past

Table 1. *Parameter estimates of threshold autoregressive models*

(The models are SETAR models based on Tong (1993), applied to series of yearly growth rates of lemmings at Finse, South Norway, 1970–1995, based on fall catches from two grids (H, M). Symbols for coefficients are the same as in equation (1) of the main text. 95% C.I. indicates the 95% confidence intervals for the growth rates at the threshold for the respective regimes ( $r_i(\beta)$ ), based on the pooled variances.)

| grid | regime<br><i>i</i> | coefficients |           |           |           | 95% C.I.<br>of $r_i(\beta)$ | <i>n</i> | threshold | pooled<br>variance | AIC <sub>c</sub> |
|------|--------------------|--------------|-----------|-----------|-----------|-----------------------------|----------|-----------|--------------------|------------------|
|      |                    | $a_{i,0}$    | (±SE)     | $a_{i,1}$ | (±SE)     |                             |          |           |                    |                  |
| H    | 1                  | 0.4266       | (±0.1441) |           |           | (0.1094, 0.7438)            | 12       | 0.10      | 0.3104             | −0.5602          |
|      | 2                  | 2.0372       | (±0.4669) | −2.7399   | (±0.4897) | (1.3492, 2.1470)            | 11       |           |                    |                  |
| M    | 1                  | 0.0830       | (±0.0766) |           |           | (−0.1044, 0.2704)           | 7        | 0.05      | 0.2536             | −0.9957          |
|      | 2                  | 1.0944       | (±0.2123) | −1.7489   | (±0.2537) | (0.8251, 1.1867)            | 16       |           |                    |                  |

densities during the upper regime represent the (delayed) density-dependence. Phase-dependence has been suggested on the basis of many earlier experimental studies (summarized by Krebs (1978)), but has never before been shown for time series data on microtines.

Our general second-order model formulation (equation (2)) may, in its deterministic form, exhibit a wide range of dynamics, from stable points via limit cycles to chaos, depending on parameter values (T. Lindström & N. C. Stenseth, unpublished data). The most appropriate model for our data (equation (3)) is, however, more restrictive. It yields interesting limit cycle behaviour with both direct and delayed density-dependence. It should be emphasized that the limited sample size of 25 growth rates severely restricts the power and reliability of the statistical analyses, as most of the methods have been developed and tested for much larger sample sizes. Nevertheless, the consistency of the results and their clear relationship to the empirical data (cf. figure 3) indicate to us that the analyses have captured some real properties of the data.

References to limit cycles abound in theoretical ecology texts. Commonly this is exemplified by the periodic fluctuations of abundances seen in northern vertebrates (e.g. Stenseth 1977, 1985; May 1981). However, except for the Canadian lynx (*Lynx canadensis*) (Tong 1993) such limit cycles have not been demonstrated in analyses of actual population time trajectories of northern microtines.

Delayed density-dependence appears to be common in northern microtines (Hanski *et al.* 1993; Turchin 1993, 1995; Hörnfeldt 1994; Bjørnstad *et al.* 1995). This is consistent with the assumption of a process influenced by specialist predators (e.g. Hanski *et al.* 1991, 1993; Hörnfeldt 1994; Bjørnstad *et al.* 1995). That such a delayed density-dependence is only observed in the upper regime conforms with recent observations that predation is important during the peak and crash phases (Norrdahl & Korpimäki 1995; Reid *et al.* 1995; Steen 1995), but sometimes absent during the low phase (Sittler 1995). In our study area Steen *et al.* (1997) demonstrate that predation is an important mortality factor (80%) in lemming carcasses found. On the basis of the time series analysis we cannot exclude that delayed effects may be due to the interactions of lemmings with their food resources

(Batzli 1992). However, current literature certainly points to predation. What seems clear, though, is that the delayed density-dependence is consistent with a significant influence of trophic interactions during the peak and crash phases.

Assuming that the density-dependent structure of the upper regime is due to predators specializing on microtines, it might seem contradictory to realize that lemmings are argued not to be highly preferred by predators (cf. Hagen 1952; Taitt 1993). However, the statistically deduced model structure is likely to apply in a community – such as ours (e.g. Østbye *et al.* 1975) – where lemmings are numerically dominant. During the low and early increase phases (when the predator density is also low) there should be no or only negligible effects of predators. Predators may increase through a numerical response to the entire rodent community (including *Microtus*); these predators will then be ‘forced’ to feed on their non-preferred prey when lemmings (and the other microtines) crash.

The significantly lower growth rate for the lower regime than for the initial part of the upper regime (table 1) indicates that maximum specific growth during the low phase (from post-peak to pre-peak year) is lower than the maximum specific growth rate (before density-dependent effects) during other phases of the cycle. This may seem paradoxical. In general, the maximum growth rate is assumed to be higher during low densities than during high densities. The experimental results of Mihok & Boonstra (1992) on *Microtus pennsylvanicus* are directly relevant in this case. They showed that voles from the low phase had poor breeding performance in ideal laboratory conditions (food, water, shelter, no predation). This poor breeding performance persisted through the F<sub>3</sub> generation in the laboratory, presumably through maternal inheritance.

Our results are important in that they incorporate intrinsic – phase-dependent – factors into population models giving rise to cycles. Earlier theoretical models which have incorporated such factors (e.g. Stenseth 1981, 1986; Stenseth & Lomnicki 1990) have generally concluded that intraspecific (and phase-dependent) factors are stabilizing, and that cycles, if they exist, do so in spite of the intrinsic stabilizing factors. Interpreting our statistical model suggests that it is the combination of intrinsic stabilizing processes coupled with destabilizing trophic processes which may be the key to untangling the puzzle of the lemming cycles.

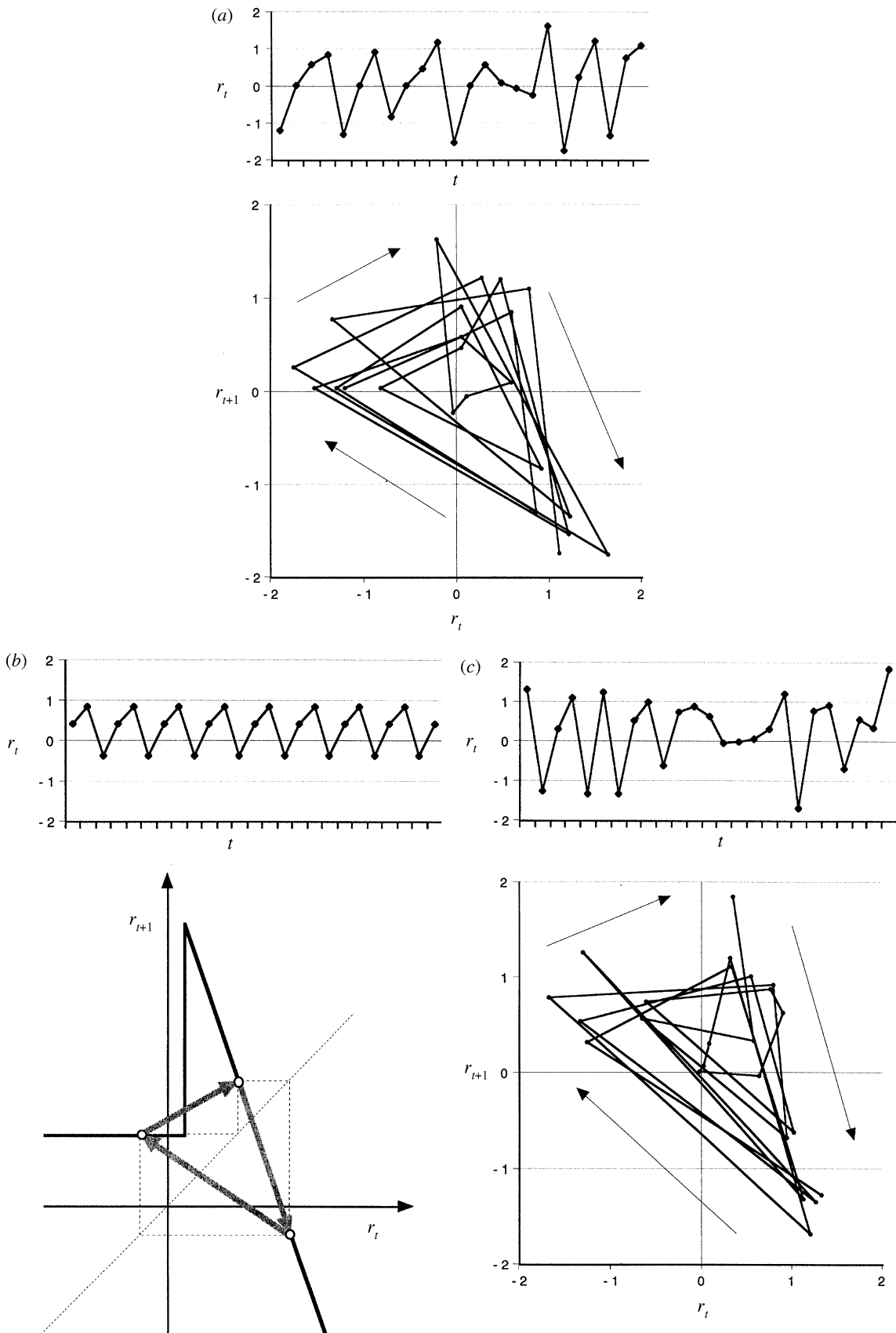


Figure 3. (a) Time plot (above) and phase plot ( $r_t$  vs  $r_{t+1}$ ) of the observed standardized growth rates for the fall series for grid H, indicating cyclic dynamics. (b) Time plot (above) and phase plot (below) of the estimated skeleton model for grid H (fall), as defined by equation (3) and with parameters as given in table 1. The model is given by the thick solid lines, while the predicted limit cycle of the growth rate (corresponding to the phase plot in (a)) is indicated by wide grey lines with arrows. (c) Time plot (above) and phase plot (below) of the estimated skeleton model for grid H (fall) with system noise (drawn from a normal distribution with mean 0 and SD of 0.50 and 0.61 as estimated from fitting the model to the original data, for the lower and upper regimes, respectively). The illustrated sequence of 25 time steps was drawn after approximately 100 time steps, well after the simulated series had stabilized.

## 6. CONCLUSION

Based on long-term data on lemming abundances in a high mountain site, we have empirically supported the hypothesis of limit cycles in lemmings. Such dynamics have long been postulated (May 1972) but has never before been demonstrated empirically. Our results contrast with recent claims that northern Fennoscandian rodents show chaotic dynamics (Hanski *et al.* 1993; Hanski & Korpimäki 1995; but see Falck *et al.* 1995*a, b*). We have furthermore found that delayed density-dependence appears to operate primarily during the peak and crash years. Intraspecific factors on the other hand are suggested to cause the differences between the specific maximum population growth rates during the post-peak (i.e. low) years and pre-peak and peak years, respectively. Thus, the growth rate of the lemmings appears to be trapped in a limit cycle, locked in the tensions between stabilizing intrinsic processes leading to self-regulation and destabilizing trophic interactions.

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 Universities of Oslo and 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. Rudy Boonstra, Ilkka Hanski, Rolf Anker Ims, Eivind Østbye, and Howell Tong have provided useful information and given helpful comments on the manuscript.

## REFERENCES

- Aune, B. 1993 Air temperature normals, normal period 1961–1990. *DNMI-Rapport 02/93 Klima*, 1–63.
- Batzli, G. O. 1992 Dynamics of small mammal populations: a review. In *Wildlife 2001: populations* (ed. D. M. McCullough & R. H. Barrett), pp. 831–850. Elsevier.
- Bjørnstad, O. N., Falck, W. & Stenseth, N. C. 1995 A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proc. R. Soc. Lond. B* **262**, 127–133.
- Borland 1992 *Borland Pascal version 7.0*. Borland International, Inc.
- Box, G. E. P. & Jenkins, G. M. 1976 *Time series analysis*. Oakland, CA: Holden-Day Inc.
- Broomhead, D. S. & King, G. P. 1986 Extracting qualitative dynamics from experimental data. *Physica D* **20**, 217–236.
- Chan, K. S. & Tong, H. 1986 On estimating thresholds in autoregressive models. *J. Time Series Anal.* **7**, 179–190.
- Chan, K. S. and Tong, H. 1990 On likelihood ratio tests for threshold autoregression. *J. R. Statist. Soc. B* **52**, 469–476.
- Charnov, E. L. & Finerty, J. P. 1980 Vole population cycles. A case for kin-selection? *Oecologia* **45**, 1–2.
- Cheng, B. & Tong, H. 1992 On consistent nonparametric order determination and chaos. *J. R. Stat. Soc. B* **54**, 427–449.
- Chitty, D. 1960 Population processes in the vole and the relevance to general theory. *Can. J. Zool.* **38**, 99–113.
- Elton, C. S. 1924 Periodic fluctuations in the numbers of animals: their causes and effects. *British J. exper. Biol.* **2**, 119–163.
- Elton, C. S. 1942 *Voies, mice and lemmings*. London: Oxford University Press.
- Falck, W., Bjørnstad, O. N. & Stenseth, N. C. 1995*a* Bootstrap estimated uncertainty of the dominant Lyapunov exponent for Holarctic microtine rodents. *Proc. R. Soc. Lond. B* **261**, 159–165.
- Falck, W., Bjørnstad, O. N. & Stenseth, N. C. 1995*b* Voies and lemmings – chaos and uncertainty in fluctuating populations. *Proc. R. Soc. Lond. B* **262**, 363–370.
- Finerty, J. P. 1980 *The population ecology of cycles in small mammals*. New Haven, CN: Yale University Press.
- Framstad, E., Stenseth, N. C. & Østbye, E. 1993*a* Time series analysis of population fluctuations of *Lemmus lemmus*. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 97–115. London: Academic Press.
- Framstad, E., Stenseth, N. C. & Østbye, E. 1993*b* Demography of *Lemmus lemmus* through five population cycles. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 116–133. London: Academic Press.
- Gilbert, N. 1984 What they didn't tell you about limit cycles. *Oecologia* **65**, 112–113.
- Hagen, Y. 1952 *Roufuglene og villpleien*. 1st edn. Oslo: Gyldendal Norsk Forlag (in Norwegian).
- Hanski, I., Hansson, L. & Henttonen, H. 1991 Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60**, 353–367.
- Hanski, I., Turchin, P., Korpimäki, E. & Henttonen, H. 1993 Population oscillations of boreal rodents: Regulation by mustelid predators leads to chaos. *Nature, Lond.* **364**, 232–235.
- Hanski, I. & Korpimäki, E. 1995 Microtine rodent dynamics in northern Europe: parameterized models for the predator–prey interaction. *Ecology* **76**, 840–850.
- Hansson, L. 1984 Winter reproduction in small mammals in relation to food conditions and populations dynamics. *Special Publ. Carnegie Museum of Natural History* **10**, 225–233.
- Hansson, L. & Henttonen, H. 1988 Rodent dynamics as community processes. *Trends Ecol. Evol.* **3**, 195–200.
- Henttonen, H. & Järvinen, A. 1981 Lemmings in 1978 at Kilpisjärvi: population characteristics of a small peak. *Mem. Soc. Fauna Flora Fennica* **57**, 25–30.
- Henttonen, H. & Kaikusalo, A. 1993 Lemming movements. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 157–186. London: Academic Press.
- Henttonen, H., McGuire, A. D. & Hansson, L. 1985 Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long term data sets of *Clethrionomys* species. *Ann. Zool. Fennici* **26**, 221–228.
- Henttonen, H., Oksanen, T., Jortikka, A. & Haukisalmi, V. 1987 How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos* **50**, 353–365.
- Heske, E. J., Ims, R. A. & Steen, H. 1993 Four experiments on Norwegian subarctic microtine rodent assemblage during a summer decline. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 411–424. London: Academic Press.
- Hjellvik, V. & Tjøstheim, D. 1995 Nonparametric tests of linearity for time series. *Biometrika* **82**, 351–368.
- Hörnfeldt, B. 1994 Delayed density dependence as a determinant of vole cycles. *Ecology* **75**, 791–806.
- Hurvich, C. M. & Tsai, C.-L. 1989 Regression and time series model selection in small samples. *Biometrika* **76**, 297–307.
- Kaikusalo, A. & Tast, J. 1984 Winter breeding of microtine rodents at Kilpisjärvi, Finnish Lapland. *Special Publication of the Carnegie Museum of Natural History* **10**, 243–252.
- Kalela, O. 1971 Seasonal differences in habitats of the Norwegian lemming, *Lemmus lemmus*, in 1959 and 1960 at

- Kilpisjärvi, Finnish Lapland. *Ann. Acad. Scient. Fenn. Ser. A, IV Biol.* **178**, 1–22.
- Kohn, R. & Ansley, C. F. 1986 Estimation, prediction, and interpolation for ARIMA models with missing data. *J. Am. Stat. Assoc.* **81**, 751–761.
- Krebs, C. J. 1964 The lemming cycle at Baker Lake, Northwest Territories, during 1959–1967. *Tech. Paper Arctic Inst. N. Am.* **15**, 1–104.
- Krebs, C. J. 1978 A review of the Chitty hypothesis of population regulation. *Can. J. Zool.* **56**, 2463–2480.
- Krebs, C. J. 1993 Are lemmings large *Microtus* or small reindeer? A review of lemming cycles after 25 years and recommendations for future work. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 247–260. London: Academic Press.
- Lack, D. 1954 *The natural regulation of animal numbers*. Oxford University Press.
- May, R. M. 1972 Limit cycles in predator–prey communities. *Science, Wash.* **177**, 900–902.
- May, R. M. (ed.) 1981 *Theoretical ecology*. 2nd edn. Oxford: Blackwell.
- Mihok, S. & Boonstra, R. 1992 Breeding performance in captivity of meadow voles (*Microtus pennsylvanicus*) from decline- and increase-phase populations. *Can. J. Zool.* **70**, 1561–1566.
- Norrdahl, K. 1995 Population cycles in northern small mammals. *Biological Reviews* **70**, 621–637.
- Norrdahl, K. & Korpimäki, E. 1995 Mortality factors in a cyclic vole population. *Proc. R. Soc. Lond. B* **261**, 49–53.
- Oksanen, L. & Oksanen, T. 1992 Long-term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos. *Ecography* **15**, 226–236.
- Østbye, E., Berg, A., Blehr, O. *et al.* 1975 Hardangervidda. In *Structure and function of tundra ecosystems* (ed. T. Rosswall & O. W. Heal). *Ecological Bulletins* **20**, 225–264.
- Pitelka, F. A. 1973 Cyclic pattern in lemming populations near Barrow, Alaska. In *Alaskan arctic tundra* (ed. M. E. Britton). *Arctic Inst. N. Am., Tech. Paper* **25**, 199–216.
- Pitelka, F. A. & Batzli, G. O. 1993 Distribution, abundance and habitat use by lemmings on the north slope of Alaska. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 213–236. London: Academic Press.
- Reid, D. G., Krebs, C. J. & Kenney, A. 1995 Limitation of collared lemming population growth at low density by predation mortality. *Oikos* **73**, 387–398.
- Royama, T. 1992 *Analytical population dynamics*. London: Chapman & Hall.
- Semb-Johansson, A., Engh, C. E. & Østbye, E. 1993 Reproduction, litter size and survival in a laboratory strain of the Norwegian lemming (*Lemmus lemmus*). In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 329–337. London: Academic Press.
- Sen, A. & Srivastava, M. 1990 *Regression analysis*. New York: Springer-Verlag.
- Sittler, B. 1995 Response of stoats (*Mustela erminea*) to a fluctuating lemming (*Dicrostonyx groenlandicus*) population in North East Greenland: preliminary results from a long-term study. *Ann. Zool. Fennici* **32**, 79–92.
- Statistical Sciences, I. 1993 *S-plus for windows version 3.2 supplement*. Seattle, WA: Statistical Sciences Inc.
- Steen, H. 1995 Untangling the causes of disappearance from a local population of root voles, *Microtus oeconomus*: a test of the regional synchrony hypothesis. *Oikos* **73**, 65–72.
- Steen, H., Holst, J. C., Solhøy, T., Bjerga, M., Klaussen, E., Prestegard, I., Sundt, R. C. & Johannesen, Ø. 1997 Mortality of lemmings (*Lemmus lemmus*) at peak density in a mountainous area of Norway. *J. Zool.* (In the press.)
- Stenseth, N. C. 1977 Evolutionary aspects of demographic cycles: the relevance of some models of cycles for microtine fluctuations. *Oikos* **29**, 525–538.
- Stenseth, N. C. 1981 On Chitty's theory for fluctuating populations: the importance of genetic polymorphism in the generation of regular cycles. *J. theor. Biol.* **90**, 9–39.
- Stenseth, N. C. 1985 Models of bank vole and wood mouse. *Symp. zool. Soc. Lond.* **55**, 339–376.
- Stenseth, N. C. 1986 On the interaction between stabilizing social factors and destabilizing trophic factors in small rodent populations. *Theor. Popul. Biol.* **29**, 365–384.
- Stenseth, N. C. 1995 Snowshoe hare populations: squeezed from below and above. *Science, Wash.* **269**, 1061–1062.
- Stenseth, N. C. & Ims, R. A. 1993a The history of lemming research: from the Nordic Sagas to *The Biology of lemmings*. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 3–34. London: Academic Press.
- Stenseth, N. C. & Ims, R. A. 1993b Population dynamics of lemmings: temporal and spatial variation – an introduction. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 61–96. London: Academic Press.
- Stenseth, N. C. & Ims, R. A. 1993c Food selection, individual growth and reproduction – an introduction. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 263–280. London: Academic Press.
- Stenseth, N. C. & Lomnicki, A. 1990 On the Charnov–Finerty hypothesis: the unproblematic transition from docile to aggressive and the problematic transition from aggressive to docile. *Oikos* **58**, 234–238.
- Sugihara, G. & May, R. M. 1990 Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. *Nature, Lond.* **344**, 734–741.
- Taitt, M. J. 1993 Adaptive coloration in *Lemmus lemmus*: why aren't Norwegian lemmings brown? In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims), pp. 439–445. London: Academic Press.
- Tjøstheim, D. 1994 Non-linear time series: A selective review. *Scand. J. Statist.* **21**, 97–130.
- Tong, H. 1983 Threshold models in nonlinear time series analysis. Lecture notes in statistics 21. New York: Springer-Verlag.
- Tong, H. 1993 *Non-linear time series*. Oxford: Clarendon.
- Tong, H. & Lim, K. S. 1980 Threshold regression, limit cycles and cyclic data (with discussion). *J. R. Statist. Soc. B* **42**, 245–292.
- Tsay, R. S. 1988 Non-linear time series analysis of blowfly population. *J. Time Series Anal.* **9**, 247–263.
- Turchin, P. 1993 Chaos and stability in rodent population dynamics: evidence from nonlinear time-series analysis. *Oikos* **68**, 167–172.
- Turchin, P. 1995 Chaos in microtine populations. *Proc. R. Soc. Lond. B* **262**, 357–361.
- Turchin, P. & Millstein, P. J. A. 1993 *EcoDyn/RSM Response surface modeling of nonlinear ecological dynamics*. Setauket, NY: Applied Biomathematics.
- Wei, W. W. S. 1990 *Time series analysis*. Redwood City, CA: Addison-Wesley.

Received 12 June 1996; accepted 5 August 1996