

# Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies

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## SUMMARY

Current ecological information on periodically fluctuating microtine populations are demonstrated to support a hypothesis involving both predation and intrinsic self-regulation as necessary and sufficient factors for explaining the 'microtine density cycle'. The structure of the cyclic time series is largely two dimensional with strong delayed density dependence. Together with recent field studies on rodent demography, our modelling suggests that trophic interaction is a likely candidate to generate the dimensionality observed for northern microtine rodent dynamics. It is shown that the trophic interaction must be fairly strong. This suggests that specialist predation is the most likely one among the classes of trophic interactions. We also argue that some – but not too strong – self-regulation must occur to generate the structure of the available time series on northern European microtines.

## 1. INTRODUCTION

"Some of us see the universe as a puzzle, and some see it as a mystery. To the puzzle solvers, why anyone seeks mystery is a puzzle indeed." (Brewer 1992)

"The study of microtine dynamics has been schismatic. Food has had its supporters, so have predation, group selection, endocrine shock, and genetic oscillations. There are shades and variations of vole cult worthy of study by an anthropologist." (Rosenzweig & Abramsky 1980)

Building upon Collett's (1911–1912) pioneering observations, Elton (1924) initiated the now extensive work on the 'microtine density cycle' (Stenseth & Ims 1993*a*; Stenseth 1995*a*). Today, we know that many northern microtines in the Palearctic zone exhibit periodic multi-annual fluctuations in the northern part of their range (recently reviewed by Stenseth & Ims 1993*b*). In Fennoscandia, for instance, most microtine populations north of about 60° N are cyclic whereas conspecific populations further south exhibit only seasonal fluctuations (Hansson 1971; Henttonen *et al.* 1985; Hansson & Henttonen 1985*a, b*; Hansson & Henttonen 1988). As going North within the cyclic region (i.e. north of 60° N), both amplitude and period of the fluctuations increase (Hanski *et al.* 1991; Bjørnstad *et al.* 1995).

In this paper we synthesise insights from pattern-oriented studies on the dynamics in time and space (cf. Hansson 1988) with insights from process-oriented studies (or 'mechanistic studies'; cf. Krebs 1988). Specifically, we derive our synthesis by expressing the parameters of the most parsimonious statistical models for microtine time series data from fennoscandia (Bjørnstad *et al.* 1995) in terms of the parameters of a mathematical model with self-regulation and trophic

interactions (see, for example, May 1973; see also Stenseth 1986). A synthesis is reached by combining these results with insights on processes known to influence the dynamics of microtines. We start by providing a synoptic summary of these processes.

Following the publication of the hypothesis by Chitty and the related one put forth by Voipio (Chitty 1952, 1957, 1960, 1967, 1996; Krebs 1978, 1979, 1996; Voipio 1950, 1988; see also Stenseth & Ims 1993*a*), and the hypothesis of Charnov & Finerty (1980; see also Charnov 1981), much effort was devoted to the investigation of social organization and spacing behaviour in microtines (Christian 1950, 1980; Krebs *et al.* 1973; Jannett 1978; Wolff 1980, 1994, 1995; Bekoff 1981; Mihok 1981; Saitoh 1981, 1991; Hestbeck 1982, 1987, 1988; Boonstra & Rood 1983; Krebs 1985, 1992, 1996; Blaustein *et al.* 1987; Boonstra & Boag 1987, 1992; Ims 1987*a, b*, 1988, 1989; Kawata 1987, 1990; Boonstra & Hogg 1988; Rodd & Boonstra 1988; Waldeman 1988; Löfgren 1989, 1995*a, b*; Ylönen 1989; Heske & Bondrup-Nielsen 1990; Lambin & Krebs 1991*a, b*, 1993; Mihok & Boonstra 1992; Ostfeld 1992*a, b*; Lambin 1993, 1994; Boonstra 1994; Wolff *et al.* 1994; for reviews, see for example Krebs & Myers 1974; Taitt & Krebs 1985; Cockburn 1988; Stenseth & Ims 1993*b*).

Below we refer to the general view that population intrinsic factors (like social and spatial organization) generate population cycles, as the population-intrinsic position. The consensus from the wealth of empirical (*op. cit.*) as well as theoretical studies (Stenseth 1977, 1981, 1986; Stenseth *et al.* 1988; Stenseth & Lomnicki 1990), is that intrinsic processes alone cannot generate the microtine density cycle. Rather, most population intrinsic processes seem to enhance stability.

Table 1. *Time series and their dimension estimates for 19 data sets North of 60° N in Europe/Fennoscandia*

(Species denote the species (Genera are abbreviated as: L = *lemmus*, C = *Clethrionomys*, M = *Microtus*). (a) Give the dimension estimates for the nonparametric order estimator of Cheng & Tong (1992) modified to use the local linear estimator of Yao & Tong (1994; see also Fan 1992). A leave-one-out cross-validation is employed on normalized, detrended, log-transformed data. Thus the CV values can be interpreted as the percentage of unpredictable variation. The optimal dimension is given by  $d_{opt}$ . When  $d_{opt}$  is different from two, the difference in explanatory power of the optimal and the two dimensional model is given ( $\Delta CV$ ). The sources of the data are indicated. Indicated below; see Falck *et al.* (1995b) for full details. (b) The crossvalidation for the linear autoregressive model. The interpretation of the values are the same as in (a). The difference is that the parametric linear model has been employed. The maximum likelihood estimates for the linear model with one data point removed using a Kalman filter applied to the state space representation of the likelihood are used (Kohn & Ansley 1986; Statistical Sciences 1993). The estimated coefficients for the 2<sup>nd</sup> order linear autoregressive model are also given. For 15 of the series these are the same as estimated by Bjørnstad *et al.* (1995; although the estimation method of SAS/ETS is slightly different from that of S-plus).

(a) *Nonlinear*

pop. no.	species	location	geographic coordinates		years	$d_{opt}$	$\Delta CV$	CV for different values of $d$					source	
			latitude	longitude				1	2	3	4	5		
1	<i>L. lemmus</i>	Finse (H)	60° 36' N	07° 30' E	1970-1994	4	-0.03	0.81	0.58	0.68	<b>0.55</b>	0.68	0.68	1
2	<i>L. lemmus</i>	Finse (M)	60° 36' N	07° 30' E	1970-1994	2		0.93	<b>0.72</b>	0.81	0.82	0.86	0.86	1
3	Microtus spp.	Finse (H)	60° 36' N	07° 30' E	1970-1994	2		0.96	<b>0.59</b>	0.63	0.76	0.82	0.82	1
4	Microtus spp.	Finse (M)	60° 36' N	07° 30' E	1970-1994	3	-0.04	0.94	0.52	<b>0.49</b>	0.50	0.54	0.54	1
5	<i>C. glareolus</i>	Boda	61° 32' N	16° 52' E	1961-1988	2		1.05	<b>0.52</b>	0.66	0.68	0.70	0.70	2
6	Microtus spp.	Alajoki	63° 05' N	22° 55' E	1977-1992	2		0.91	<b>0.69</b>	0.92	1.27	1.25	1.25	3
7	Microtus spp.	Ruotsala	63° 09' N	23° 09' E	1973-1992	3	0.00	0.95	0.50	<b>0.50</b>	0.56	0.71	0.71	3
8	<i>C. glareolus</i>	Umeå	63° 50' N	20° 15' E	1971-1991	2		1.15	<b>0.83</b>	1.05	0.96	0.95	0.95	4
9	<i>C. rufocanus</i>	Umeå	63° 50' N	20° 15' E	1971-1992	2		1.05	<b>0.25</b>	0.27	1.01	0.77	0.77	4
10	<i>M. agrestis</i>	Umeå	63° 50' N	20° 15' E	1971-1993	4	-0.11	0.83	0.54	0.54	<b>0.43</b>	0.71	0.71	4
11	<i>C. glareolus</i>	Sotkamo	64° 08' N	28° 25' E	1966-1992	2		1.01	<b>0.90</b>	0.98	1.32	1.28	1.28	5
12	<i>M. agrestis</i>	Sotkamo	64° 08' N	28° 25' E	1966-1992	3	-0.04	0.95	0.80	<b>0.76</b>	0.85	0.95	0.95	5
13	<i>C. rufocanus</i>	Kola	67° 55' N	32° 50' E	1974-1992	3	-0.08	1.06	0.10	<b>0.02</b>	0.12	0.13	0.13	6
14	<i>C. glareolus</i>	Pallasjärvi	68° 03' N	24° 09' E	1970-1992	2		1.01	<b>0.94</b>	1.00	1.14	1.35	1.35	7
15	<i>C. rufocanus</i>	Pallasjärvi	68° 03' N	24° 09' E	1970-1992	3	-0.02	1.13	0.69	<b>0.67</b>	0.87	1.05	1.05	7
16	<i>C. rutilus</i>	Pallasjärvi	68° 03' N	24° 09' E	1970-1992	2		1.20	<b>0.98</b>	1.03	1.13	1.29	1.29	7
17	<i>C. glareolus</i>	Kola	68° 53' N	33° 02' E	1946-1964	2		1.03	<b>0.85</b>	0.96	1.00	1.29	1.29	8
18	<i>C. glareolus</i>	Kola	68° 53' N	33° 02' E	1946-1964	2		0.97	<b>0.47</b>	0.78	0.82	0.90	0.90	8
19	<i>C. rufocanus</i>	Kilpisjärvi	69° 03' N	20° 48' E	1949-1970	2		1.08	<b>0.42</b>	0.52	0.75	0.74	0.74	9
20	<i>C. rufocanus</i>	Kilpisjärvi	69° 03' N	20° 48' E	1971-1992	4	-0.20	1.13	0.75	0.73	<b>0.55</b>	0.88	0.88	9

(b) *Linear*

pop. no.	species	geographic coordinates			years	d <sub>opt</sub>	ΔCV	AR-coeff.		CV for different values of d <sup>a</sup>					source
		location	latitude	longitude				a <sub>1</sub>	a <sub>2</sub>	1	2	3	4	5	
1	<i>L. lemmus</i>	Finse(H)	60° 36' N	07° 30' E	1970-1995	2		-0.48	-0.62	0.82	<b>0.49</b>	0.52	0.49	0.59	1
2	<i>L. lemmus</i>	Finse(M)	60° 36' N	07° 30' E	1970-1995	2		-0.38	-0.57	0.83	<b>0.62</b>	0.66	0.63	0.67	1
3	Microtus spp.	Finse(H)	60° 36' N	07° 30' E	1970-1995	2		-0.30	-0.57	0.70	<b>0.48</b>	0.53	0.58	0.55	1
4	Microtus spp.	Finse(M)	60° 36' N	07° 30' E	1970-1995	3	-0.01	-0.48	-0.43	0.57	<b>0.38</b>	<b>0.37</b>	0.37	0.42	1
5	<i>C. glareolus</i>	Boda	61° 32' N	16° 52' E	1961-1988	5	-0.03	-0.11	-0.71	1.17	0.61	0.71	0.73	<b>0.59</b>	2
6	Microtus spp.	Alajoki	63° 05' N	22° 55' E	1977-1992	2		-0.62	-0.72	1.07	<b>0.65</b>	0.76	—	—	3
7	Microtus spp.	Ruotsala	63° 09' N	23° 09' E	1973-1992	3	-0.01	-0.61	-0.75	1.05	0.49	<b>0.48</b>	—	—	3
8	<i>C. glareolus</i>	Umeå	63° 50' N	20° 15' E	1971-1994	5	-0.02	-0.17	-0.55	0.54	0.44	0.55	0.53	<b>0.42</b>	4
9	<i>C. rufocanus</i>	Umeå	63° 50' N	20° 15' E	1971-1994	4	-0.06	-0.23	-0.63	0.82	0.52	0.60	<b>0.47</b>	0.51	4
10	<i>M. agrestis</i>	Umeå	63° 50' N	20° 15' E	1971-1994	2		-0.19	-0.71	0.79	<b>0.37</b>	0.40	0.41	0.50	4
11	<i>C. glareolus</i>	Sotkamo	64° 08' N	28° 25' E	1966-1992	4	-0.07	-0.17	-0.38	1.10	0.99	1.08	<b>0.92</b>	0.94	5
12	<i>M. agrestis</i>	Sotkamo	64° 08' N	28° 25' E	1966-1992	3	-0.09	-0.38	-0.56	0.87	0.67	<b>0.58</b>	0.68	0.86	5
13	<i>C. rufocanus</i>	Kola	67° 55' N	32° 50' E	1974-1992	4	-0.15	0.25	-0.77	1.07	0.41	0.36	<b>0.27</b>	0.27	6
14	<i>C. glareolus</i>	Pallasjärvi	68° 03' N	24° 09' E	1970-1992	2		0.09	-0.55	0.87	<b>0.62</b>	0.67	0.71	0.97	7
15	<i>C. rufocanus</i>	Pallasjärvi	68° 03' N	24° 09' E	1970-1992	2		0.34	-0.66	1.09	<b>0.67</b>	0.69	0.77	0.83	7
16	<i>C. rutilus</i>	Pallasjärvi	68° 03' N	24° 09' E	1970-1992	2		0.08	-0.57	0.94	<b>0.72</b>	0.82	0.81	1.01	7
17	<i>C. glareolus</i>	Kola	68° 53' N	33° 02' E	1946-1964	2		0.09	-0.49	0.91	<b>0.65</b>	0.72	0.77	1.22	8
18	<i>C. rufocanus</i>	Kola	68° 53' N	33° 02' E	1946-1964	2		0.12	-0.51	1.20	<b>0.90</b>	0.91	0.95	0.94	8
19	<i>C. rufocanus</i>	Kilpisjärvi	69° 03' N	20° 48' E	1949-1970	5	-0.07	0.22	-0.63	0.83	0.53	0.48	0.48	<b>0.46</b>	9
20	<i>C. rufocanus</i>	Kilpisjärvi	69° 03' N	20° 48' E	1971-1992	3	-0.04	0.12	-0.60	1.00	0.63	0.74	0.66	0.66	9

<sup>a</sup> '—' indicate situations with no convergence.

(1) Framstad *et al.* (1993); (2) Marström *et al.* (1990); (3) Korpimäki & Norrdahl (1991*b*), Korpimäki (1993, 1994); (4) Hörnfeldt (1994); (5) Henttonen *et al.* (1977), A. Kalkusalo (personal communication); (6) Kataev *et al.* (1994); (7) Henttonen *et al.* (1977, 1987), Hanski & Henttonen (1996), H. Henttonen (personal communication); (8) Koshkina (1966) (provided by P. Turchin); and (9) Kalela (1957), Laine & Henttonen (1983, 1987), H. Henttonen (personal communication).

Before the focus on behaviour and other intrinsic factors, much attention was devoted to population extrinsic factors, in particular trophic interactions, as responsible for population cycles (Hagen 1952; Pitelka *et al.* 1955; Kalela 1957, 1961, 1962; Pitelka 1958, 1964; Schultz 1964, 1969; Pearson 1964, 1966). This view we refer to as the community-level position (Hansson & Henttonen 1988). Gradually there has been a return in focus to such extrinsic processes, particularly that of predation (MacLean *et al.* 1974; Fitzgerald 1977; Erlinge *et al.* 1983, 1984; Angelstam *et al.* 1984; Erlinge 1987; Hanski 1987; Hansson 1987; Henttonen *et al.* 1987; Sonerud 1988; Desy & Batzli 1989; Korpimäki & Norrdahl 1989, 1991 *a, b*; Desy *et al.* 1990; Steen *et al.* 1990; Korpimäki *et al.* 1991, 1994; Korpimäki 1993, 1994; Norrdahl & Korpimäki 1993, 1995 *a, b*; Norrdahl 1995; Korpimäki & Krebs 1996). A series of independent studies on predation on microtines (Norrdahl & Korpimäki 1995 *a*; Reid *et al.* 1995; Steen 1995; see also Heske *et al.* 1993), indicate that predators represent a key to understanding the mortality associated with the microtine cycle (but see Krebs (1996) who states that 'predation does not seem to be either necessary or sufficient to generate a cycle in these small mammals'). Predators specializing on rodents (e.g. mustelids and owls) are, as a result, seen by some researchers as the solution to the cycle (see, for example, Hanski *et al.* 1991, 1993; Hanski & Korpimäki 1995).

Many authors focusing on predation as a key factor in the generation of the cycle, view predation as an alternative to intrinsic hypotheses. Thus, the population-intrinsic position and the community-level position are commonly seen as representing opposing hypotheses. In this paper we argue that the presumed dichotomy between the intrinsic- and community position is not an appropriate interpretation of available empirical and theoretical results. Indeed, we suggest that both community-level and population-intrinsic factors are necessary for generating population dynamics of the kind seen in the 'microtine cycle'. In addition, we argue that a trophic interaction involving specialist predation coupled with some self-regulatory factor are sufficient for explaining the microtine cycle. We are certainly not the first to propose such a combined view (Taitt & Krebs 1985; Bondrup-Nielsen & Ims 1988 *a, b*; Heske & Bondrup-Nielsen 1990; Krebs 1995, 1996). We do, however, demonstrate the validity of such a view on the basis of recent empirical and theoretical studies.

## 2. A METHODOLOGICAL PREAMBLE

The density dependent paradigm assumes that the numerical dynamics of a population may be approximated by a model of the form

$$N_t = \Theta(N_{t-1}, \dots, N_{t-d}) + \epsilon_t, \quad (1)$$

where  $\Theta$  is some function – or model – (linear or nonlinear) and  $\epsilon_t$  is the effect of environmental or demographic stochasticities. Classically,  $d$  is assumed to be one, and the stochasticity is assumed negligible (see, for example, May 1976; May & Oster 1976; Bellows

1981). Only occasionally is stochasticity explicitly incorporated in the models (Braumann 1983; Dennis & Patil 1984; Dennis *et al.* 1995). Higher dimensional models ( $d > 1$ ), stochastic or deterministic, generally arise for three biological reasons (Royama 1992; see also Gilbert 1993): developmental delays (May 1981; MacDonald 1989), age-size structure (Ebenman & Persson 1988), and interspecific interactions (Maynard Smith 1974; Maynard Smith & Slatkin 1978; Royama 1981; Stenseth 1995 *b*; Stenseth *et al.* 1996 *b*).

Ecologists attempt to infer the processes that control the dynamics of populations. One approach may be to try to reconstruct the model  $\Theta(\cdot)$  on the basis of time series data (see, for example, Tong 1990; Royama 1992). In §3 we summarise studies on cyclic microtine rodents taking such a statistical approach. A second approach is to develop mathematical models for population dynamics (see, for example, May 1973; Maynard Smith 1974; Caswell 1989; Yodzis 1989). In §4 we discuss this approach with reference to cyclic microtine rodents. Despite both approaches relating to the same phenomenon, their insights are only rarely merged. With reference to cyclic microtine rodents, we attempt such a synthesis in §5.

## 3. STATISTICAL MODELLING OF MICROTINE TIME SERIES

Equation (1) is a nonlinear autoregressive model. A sensible first step in reconstructing the underlying model,  $\Theta(\cdot)$ , is to estimate the ecological dimension (or what the statisticians call the order of the process; see, for example, Cheng & Tong 1992). This is a non-trivial problem. A classical simplification is to assume that  $\Theta(\cdot)$  [or  $\Theta(\cdot)/N_t$ ] is a linear function in  $(N_{t-1}, N_{t-2}, \dots, N_{t-d})$  (Hurvich & Tsai 1989; Wei 1990; Royama 1992; see also Lotka 1925; Volterra 1926; May 1972, 1973, 1981; Maynard Smith 1974). However, if we assume linearity in  $\Theta$  when the true  $\Theta$ -function is nonlinear, we often overestimate the dimension of the dynamics (cf. Takens theorem: Broomhead & Jones 1989). A frequently employed alternative therefore is to assume that  $\Theta$  is a nonlinear parametric function in  $N$  (see, for example, Hassell *et al.* 1976; Berryman 1991; Turchin 1993; Turchin &

Table 2. *Definition of the degree of the ecological interactions in equation (5) at equilibrium*

(The 'other-than-vole' trophic level is referred to as the 'y-level' (interpreted in the conclusion of the paper as 'specialist vole predators'.)

type of ecological interaction	symbol
Vole's growth rate in absence of self-regulation and the other trophic level ( $\alpha_{10}$ )	$\alpha_{10} = f(0,0)$
self-regulation in voles ( $\alpha_{11}$ )	$\alpha_{11} = \partial f / \partial x$
effect of y-level on voles ( $\alpha_{12}$ )	$\alpha_{12} = \partial f / \partial y$
the y-level's growth rate in absence of self-regulation and voles ( $\alpha_{20}$ )	$\alpha_{20} = g(0,0)$
self-regulation in the y-level ( $\alpha_{22}$ )	$\alpha_{22} = \partial g / \partial y$
effect of voles on the y-level ( $\alpha_{21}$ )	$\alpha_{21} = \partial g / \partial x$

Table 3. The autoregressive parameters in the model defined by equation (3) as functions of the ecological parameters in the model defined by equation (5)

autoregressive parameter	ecological model	features of the Jacobian (J) (mathematical interpretations)
$a_0$	$\alpha_{20} \cdot \alpha_{12} - \alpha_{10} \cdot \alpha_{22}$	determining the equilibrium of $x_t$
$a_1$	$\alpha_{11} + \alpha_{22} + 2$	trace(J)
$a_2$	$\alpha_{12} \cdot \alpha_{21} - \alpha_{11} \cdot \alpha_{22} - \alpha_{11} - \alpha_{22} - 1$	-determinant(J)

Millstein 1993). Unfortunately, when our preconception is in error our conclusion will, to some extent, be an artefact of our prejudices rather than the truth about nature. Hence, we should ideally use a non-parametric model to estimate this dimension,  $d$ , of population dynamics. In this way the error is likely to be reduced (Cheng & Tong 1992). A suitable non-parametric way of estimating  $\Theta(\cdot)$  is to use a smoother such as the weighted local linear regression of Fan (1992; see also Yao & Tong 1994) with a product Gaussian kernel (Tarter & Lock 1993).

The appropriate dimension of the population dynamics, may be seen as that of the model that predicts the dynamics the best (Stone 1977). We use the 'leave-one-out' cross validation method for estimating  $d$  (see, for example, Stone 1977; Cheng & Tong 1992; Efron & Tibshirani 1993). The idea is to remove one data-point from the time series and estimate the model based on the remaining observations. A regression model will then be used to predict the deleted point. The process is repeated for all data points in the time series. The mean sum of squared differences, is the CV-value for the dimension of the non-parametric model. We repeat this for each dimension  $\{1, \dots, d_{\max}\}$ . The  $d$  that minimizes the CV, is the parsimonious dimension estimate of Cheng & Tong (1992). A word of caution is in order, however: typically an ecological time series is short. Any estimate is therefore going to be associated with substantial uncertainty (Falck *et al.* 1995 *a, b*).

Table 1 summarizes the analysis of the available Fennoscandian time series with respect to dimensionality, both assuming a non-parametric nonlinear autoregressive model (table 1*a*) and a linear autoregressive model (table 1*b*). The original time series data were in both cases log-transformed to stabilize the variance (for examples, see Sen & Srivastava 1990; Bjørnstad *et al.* 1995); that is, we use  $x_t = \ln(N_t + \text{small constant})$ . This transformation is furthermore biologically sensible because of the multiplicative nature of birth and death processes (for examples, see Lebreton 1989; Broekhuizen & McKenzie 1995). The log-transformed series have been scaled to have zero mean and variance equal to one. To avoid spurious results caused by trends in time series, all log-transformed series were detrended using a scatterplot smoother (LOWESS; Statistical Sciences 1993) with band width equal to six (being just longer than the longest period reported for microtine cycles).

Using non-parametric regression (table 1*a*), it can be seen that most (60%) of the northern time series were estimated to have dimension of two. A total of five of the series which were not estimated to have dimension two, gave only a negligible less fit (5%) by

assuming dimension two: thus 85% of the northern time series on microtine rodents have approximately dimension two. The only exceptions from this two-dimensional structure are *Clethrionomys rufocanus* at Kilpisjärvi in the series after 1970 (a series which is considered non-stationary and non-cyclic by Henttonen (personal communication) and Hanski & Henttonen (1996)), *Microtus agrestis* outside Umeå (both of which were found to have dimension four), and *Clethrionomys rufocanus* from Kola. Cross-validating the linear model, slightly more series are found to have dimension larger than two as their overall best estimate (table 1*b*). However, this may be expected in the presence of nonlinearities. Nevertheless, using the 5% criterion, 14 (70%) are consistent with  $d=2$ . In conclusion, considering the innate uncertainty in our data, dimension two is the most appropriate dimension for the northern microtine time series. This has also been found in previous studies (Turchin 1993; Turchin *et al.* 1993; Bjørnstad *et al.* 1995). (For the Kilpisjärvi series, it is worth noticing that analysing the latter part of the series only till 1988, gives an optimal dimension equal to two both when assuming a linear and a nonlinear model.)

Assuming a two dimensional structure, we may describe these time series data, using delay coordinates, by the following model:

$$x_t = \Phi(x_{t-1}, x_{t-2}) + \epsilon_t. \quad (2)$$

The  $\Phi$ -function may take on a variety of forms, but for the purpose of studying patterns of statistical density dependence, we may specify the  $\Phi$ -function as a log-linear function of abundances (see, for example, Royama 1992; Bjørnstad *et al.* 1995):

$$x_t = a_0 + a_1 \cdot x_{t-1} + a_2 \cdot x_{t-2} + \epsilon_t. \quad (3)$$

The coefficients,  $a_i$  ( $i = 0, 1, 2$ ), can be estimated from time series data (table 1). Notice that only the autoregressive parameters  $a_1$  and  $a_2$  will influence the dynamics of the second order log-linear model (Royama 1981, 1992).

#### 4. MATHEMATICAL MODELLING OF MICROTINE POPULATION DYNAMICS

Many, but far from all, hypotheses for the rodent cycle (Stenseth & Ims 1993*b*) are consistent with the two dimensional structure of the data. For instance, the multifactorial hypothesis (Lidicker 1988; see also Gaines *et al.* 1991; Lidicker 1991) assuming cascades of interacting processes will result in higher-than-two dimensional dynamics. This expectation is not borne out in the available data (table 1). Similarly, the food

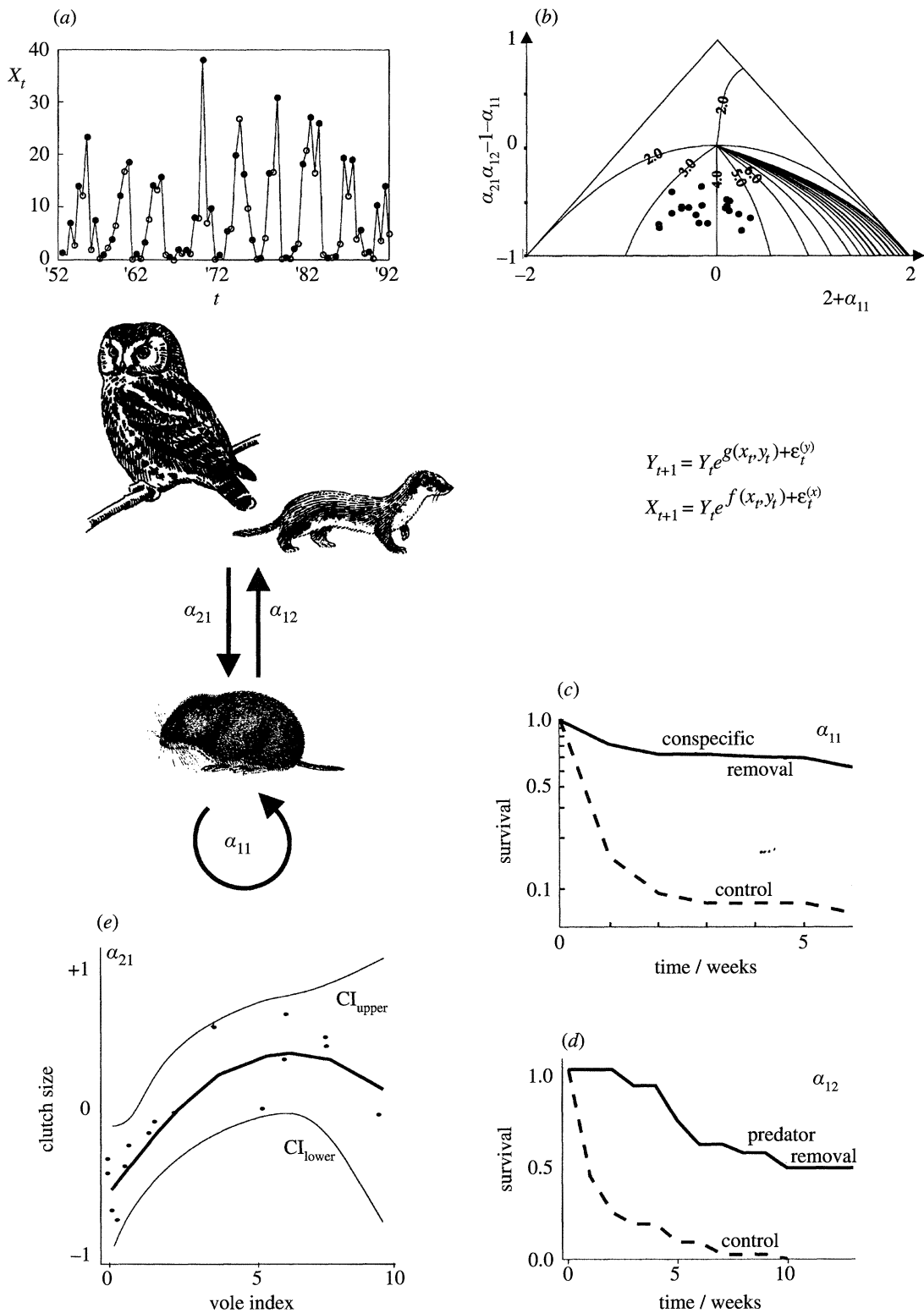


Figure 1. The 'microtine rodent cycle'. (a) The density cycles at Kilpisjärvi, Finland (Laine & Henttonen 1987; figure adapted from Hanski *et al.* 1993) are a typical example of the 3–5 year microtine density cycle. Solid circles represent spring, open circles represent fall. The period length for this very northern population is approximately 5 years. (b) Empirically, the cycles in Fennoscandia is produced by a narrow range of coefficients of delayed (vertical axis) and direct (horizontal axis) density dependence (adapted from Bjørnstad *et al.* 1995). The parameters in the population dynamic model (see text) represent the ecological interactions among the voles ( $\alpha_{11}$ ) and between the voles and their specialist predators ( $\alpha_{12}$  and  $\alpha_{21}$ ). These parameters are, as indicated on the axes, related to the statistical coefficients. The sign of the parameters can be illustrated from three recent studies: (c) Boonstra (1978) demonstrated experimentally the presence of intrinsic regulation ( $\alpha_{11}$ ) in Townsend's vole (*Microtus townsendii*). (d) Reid *et al.* (1995) demonstrated experimentally strong effects of predators on the demography of collared lemming (*Dicrostonyx groenlandicus*) ( $\alpha_{12}$ ). (e) The relation between the clutch size of the Tengmalm's owl (*Aegolius funereus*) and vole

chain hypothesis of Oksanen and coworkers (for examples, see Oksanen *et al.* 1981; Oksanen 1990, 1991; Oksanen & Oksanen 1992), predicting a dimension of three or more, may be concluded inconsistent with available data on northern microtine rodents. Henceforth, we may narrow the search to models (or hypotheses) with no more than two dynamic variables. Following the synoptic review we have provided in the introduction to this paper, we are lead to consider a trophic model. Because, density dependence in the voles appears common (Hörnfeldt 1994; Bjørnstad *et al.* 1995; Ostfeld & Canham 1995; Saitoh *et al.* 1996; Stenseth *et al.* 1996a), we should allow for self-regulation.

Let  $X_t$  be the abundance of voles at time  $t$ . Let  $Y_t$  be the abundance of a species either being a food resource for the rodent or a predator on the rodent species. A general population dynamics model for this trophic system is (see, for example, Maynard Smith 1974):

$$\begin{aligned} X_{t+1} &= X_t \cdot F(X_t, Y_t, \epsilon_t^{(x)}) \\ Y_{t+1} &= Y_t \cdot G(X_t, Y_t, \epsilon_t^{(y)}), \end{aligned} \quad (4)$$

where  $F$  and  $G$  are functions describing the ecological interactions in the system, and  $\epsilon_t^{(x)}$  and  $\epsilon_t^{(y)}$  are sequences of state independent random variables with zero mean. We may write  $F(\cdot)$  and  $G(\cdot)$  as exponential functions (see, for example, Stenseth *et al.* 1996a):

$$\begin{aligned} X_{t+1} &= X_t \cdot \exp(f(x_t, y_t) + \epsilon_t^{(x)}) \\ Y_{t+1} &= Y_t \cdot \exp(g(x_t, y_t) + \epsilon_t^{(y)}), \end{aligned} \quad (5)$$

where  $f$  and  $g$  are functions in  $x_t$  and  $y_t$ , and  $x_t = \log(X_t)$  and  $y_t = \log(Y_t)$ ; essentially this is a general Gompertz model (Gompertz 1825; see also Lebreton 1989).

Table 2 summarises the ecological interpretation of the partial differentials of  $f$  and  $g$  around the equilibrium (denoted by  $\alpha_{ij}$  which represent the influence of species  $j$  on species  $i$ ; May 1973). The functions  $f$  and  $g$  (as well as  $F$  and  $G$ , etc.) are the biological functions; their parameters are referred to as the biological parameters of the system. The results of the statistical modelling (see §3) constrain these functions to identify permissible ranges of values for the interaction coefficients  $\alpha_{ij}$  (see table 3).

## 5. LINKING MATHEMATICAL MODELS AND STATISTICAL AUTOREGRESSIVE MODELS

The ecological model discussed in §4 may be linked directly with the statistical models of table 1 (§3). In the case of log-linearity in  $f(\cdot)$  and  $g(\cdot)$ , the partial differentials (table 2) will uniquely define the parameters of the log-linear autoregressive model (equation (3)).

As can be seen from table 3a, the first order autoregressive parameter ( $a_1$ ) is solely determined by the self-regulating processes (of which there is a whole array in rodents such as territoriality, density dependent maturation, and density dependent dispersal; see §1) in the two interacting species. Notice that  $\alpha_{11}$  even include mortality caused by an instantaneous functional response of generalist predators (Hassell & May 1986; Bjørnstad *et al.* 1995). The second order autoregressive ( $a_2$ ) parameter is a compound function of different processes in the ecological system. As a result,  $a_2$  may take on a variety of values (positive as well as negative). The value of  $a_2$  depends upon the relative strength of trophic interaction ( $\alpha_{12} \alpha_{21}$ ) versus self-regulation ( $\alpha_{11}$  and  $\alpha_{22}$ ).

Bjørnstad *et al.* (1995) show that for cyclic Fennoscandian microtines,  $a_1$  vary between  $-0.6$  and  $0.3$  (southern cyclic populations being approximately equal to  $-0.6$  and northern populations being approximately equal to  $0.3$ ), and  $a_2$  is approximately constant at  $-0.6$ . The parameter estimates for these, as well as a few series more recently brought to our attention, are given in table 1 (note that the exact estimates varies slightly from those of Bjørnstad *et al.* (1995) because a different statistical program was used; S-plus, version 3.2; Statistical Sciences 1993). The results imply (table 1), that:

$$-2.6 < \alpha_{11} + \alpha_{22} < -1.7, \quad (6)$$

and

$$\alpha_{12} \cdot \alpha_{21} - \alpha_{11} \cdot \alpha_{22} - \alpha_{11} - \alpha_{22} = 0.4. \quad (7)$$

Substituting the relations in equation (6) into equation (7) yield:

$$-2.2 < \alpha_{12} \cdot \alpha_{21} - \alpha_{11} \cdot \alpha_{22} < -1.3. \quad (8)$$

To simplify the argument, let us first assume negligible self-regulation in the other trophic level (i.e.  $\alpha_{22} \approx 0$ ); below we relax this assumption. With the assumed simplification, the above statistically derived constraints imply:

$$-2.6 < \alpha_{11} < -1.6, \quad (9)$$

and

$$-2.2 < \alpha_{12} \cdot \alpha_{21} < -1.4. \quad (10)$$

Equation (9) is consistent with a fairly strong degree of self-regulation ( $\alpha_{11}$ ) in the vole populations. Thus, the analysis of available long-term time series on northern microtine populations in Fennoscandia (as exemplified by figure 1a) support the conclusion of the population intrinsic hypotheses: self-regulatory processes (including spacing behaviour) are important. Certainly, all studies on spacing behaviour in microtines (cf. §1) imply  $\alpha_{11}$  to be negative (figure 1c).

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abundance showing a clear effect of voles on the predators ( $\alpha_{21}$ ) (reanalysis of data presented in table 1 of Korpimäki & Hakkarainen (1991)). The figure depicts the generalised additive (non-parametric) regression model (Hastie & Tibshirani 1990; Statistical Sciences 1993) using a spline smoother with 2 degrees of freedom, identity link and quasi-Poisson variance function for number of eggs versus vole index ( $p = 0.07$ ); the upper and lower 95% confidence interval is shown. The relation has been corrected for laying date. (Similar observations are provided by Korpimäki & Lagerström (1988) and Hörnfeldt *et al.* (1990).)

Equation (10), furthermore, is consistent with a specialist predator influencing the dynamics of the voles: for specialist predators, both the influence of voles on the predators growth rate ( $\alpha_{21}$ ) and the effect of the predators on the voles growth rate ( $\alpha_{12}$ ) are strong, one being negative ( $\alpha_{12}$ ) and one being positive ( $\alpha_{21}$ ) rendering the product strongly negative.

Another trophic candidate would be a plant-herbivore interaction. However, the little relevant evidence that exist (Batzli 1983, 1992; Laine & Henttonen 1983, 1987; Seldal *et al.* 1994) does not indicate  $\alpha_{21}\alpha_{12}$  to be sufficiently negative in such interactions: this needs further testing, though. On the basis of available observational and experimental data, we are lead to conclude that the time series of northern microtines are consistent with the 'community-level position'. This is particularly so because of the recent field studies on vole predation (Steen 1995; Norrdahl & Korpimäki 1995*a*; Reid *et al.* 1995) demonstrating that  $\alpha_{12}$  is negative (figure 1*d*; that is, predatory induced mortality is not compensatory in voles). By definition,  $\alpha_{21}$  will be positive for specialist predators (figure 1*e*), but approximately zero for generalists.

If we relax the assumption of  $\alpha_{22} \approx 0$  (no self-regulation in the predator), we see (equation 6) that the self-regulation in the vole population need not be as strong, nor need the interaction between the trophic levels ( $\alpha_{12} \cdot \alpha_{21}$ ) be as strong. Thus, if both trophic levels are self-regulated, equation (8) might be satisfied even for  $\alpha_{12} \cdot \alpha_{21}$  not highly different from zero (which could be the case for generalist predation or plant-herbivore interactions). This will need further investigation (but see Lockie 1961; King 1989).

## 6. A SYNTHETIC HYPOTHESIS

In summary, we argue that all currently available empirical information, both from experimental studies like those reviewed by Krebs (1978, 1993, 1996) and analysis of population trajectories (Bjørnstad *et al.* 1995: figure 1*b*), are consistent with the microtine cycle resulting from both trophic interactions and self-regulation. The microtine density cycle seems to be caused by the combination of self-regulation (such as spacing behaviour) and predation by rodent specialists. We conclude the following.

1. Some degree of self-regulation ( $\alpha_{11} < 0$ ; figure 1*c*) (mediated by factors such as spacing behaviour) seems necessary to obtain the observed microtine cycle. Population-intrinsic mechanisms are demonstrably essential for the cycles to occur. Self-regulation must not be too strong, though.

2. Small rodent specialist predators (e.g. mustelids and some owl species) are likely candidates for the other necessary factor (figure 1*d, e*). Generalist predators will result in (voles' effect on predator)  $\times$  (predator's effect on voles) being approximately equal to zero, violating the statistical results of available long-term data.

3. Thus, specialist predation and self-regulation appears necessary and may be sufficient for generating the microtine cycle.

Our hypothesis is consistent with the pattern in the available time series data on cyclic microtine rodents from Fennoscandia; most importantly (*a*) their two dimensional structure and (*b*) the permissible range of the ecological parameter values. It should be emphasized though, that our hypothesis by no means has been tested: neither has its components been indisputably demonstrated. In much current literature on cyclic small rodents (see, for example, Hanski *et al.* 1993; Hanski & Korpimäki 1995; Norrdahl 1995; Turchin & Hanski 1996), the impression is often given that the puzzle of the 'microtine cycle' is solved. The empirical basis of such a conclusion is indeed very weak. Figure 1 summarises some experimental results, but more experimental data as well as further analyses of available data is required before we can conclude causation and not only consistence.

## 7. CONCLUSION

To suggest that both population-intrinsic processes and community-level processes are essential for generating periodic fluctuations in rodents, is not new. For instance, Taitt & Krebs (1985: p. 611) suggest that a 'synthesis could be based on the premise that both extrinsic and intrinsic factors are involved in *Microtus* population fluctuations' (see also Krebs 1996). However, the empirical support for such a synthetic view has not yet been put together. Unfortunately, proponents of one or the other view, generally focus on one factor as the single most important key factor. For instance, Hanski *et al.* (1993) concluded that 'the 3–5-year small mammal cycle...is generated by delayed density dependence as a result of specialist predators' despite their model incorporating both intrinsic and extrinsic factors. This misses the critical fact that microtine rodent density cycles appears to be locked in the tension between stabilizing self-regulation and destabilising trophic interactions (May 1972; Stenseth 1986; Framstad *et al.* 1996). We differ from Hanski & Turchin and others (see, for example, Hanski *et al.* 1991, 1993; Hanski & Korpimäki 1995; Turchin & Hanski 1996) in not only emphasising specialist predation. We maintain that we need to emphasise both intrinsic processes and the extrinsic trophic processes; and that we need to understand the balance between these two classes of processes.

The jigsaw pieces seem to be on the table, and we believe we are close to putting them together to solve the puzzle that has troubled ecologists for more than 70 years. The results reported in this paper demonstrate the necessity of merging the views of the different schools of thought. It appears that in concert, both schools of microtine population dynamics is right, but missing the critical fact that the effects of self-regulation and the trophic interaction are inextricably intertwined.

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