

not necessarily cause species extinction. For suitable parameter values we have observed reductions in extinction rates up to $r = 12.0$. (4) Log-log plots of mean time to extinction, \bar{T} , versus mean time between perturbations, $\bar{\tau} = 1/p$, suggest scaling laws of the form

$$\bar{T} = A \bar{\tau}^B \quad (9)$$

For small $\bar{\tau}$, the exponent, B , is determined by the rate of trajectorial separation, that is, by the magnitude of the positive Lyapunov exponent. For large $\bar{\tau}$, B approaches an expected value of unity as the system relaxes to its invariant measure³⁶. In this case, the chaotic systems have extinction times (\bar{T}) 100 to 1,000 times greater than their non-chaotic counterparts.

The foregoing calculations suggest that species extinction is not the inevitable consequence of chaotic population dynamics that some would maintain. On the contrary, chaos can provide significant protection against extinction by increasing the degree of asynchrony among local populations. This result is consistent with recent conclusions³⁷ that subdividing a population can stabilize systems that would otherwise go extinct with probability one. In those experiments, extinction resulted from deterministic forces, whereas here, the responsible factors are stochastic. The essential mechanism is nonetheless the same: local populations become decorrelated so that when one goes extinct, recolonization by migrants prevents extinction of the whole. We have extended this discussion by pointing out that the stabilizing effects of subdivision and migration are enhanced by chaos. One possible example of 'chaos-mediated' survival is the persistence of highly contagious diseases, such as measles, in human populations below what is called the "critical community size"³⁸. Here, as in the ecological case considered above, unstable (chaotic?) dynamics induce asynchrony among local populations, thereby reducing the pathogen's chance of extinction. Potentially interesting extensions of our results include (1) the search for circumstances in which chaos reduces extinction rates at both the local and species levels, and (2) examination of the effect of chaos on extinction in spatially distributed systems of interacting species. □

36. Lichtenberg, A. J. & Leiberman, M. A. *Regular and Stochastic Motion* (Springer, New York, 1983).
 37. Yorke, J. A., Nathanson, N., Pianigiani, G. & Martin, J. *Am J. Epidem.* **109**, 103–122 (1979).
 38. Hassell, M. P., Comins, H. N. & May, R. M. *Nature* **353**, 255–258 (1991).

ACKNOWLEDGEMENTS. We thank P. Chesson, G. Fox, J. H. Frank, B. Kendall, J. Keesling, M. Kot, J. Logan, R. May, S. Schwinning, G. Sugihara, C. Tidd, P. Turchin, T. J. Walker and A. Winfree for comments and discussion. This work was supported by grants from USDA to J.C.A. and NIH to W.M.S.

Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos

Ilkka Hanski*, Peter Turchin†, Erkki Korpiimäki‡ & Heikki Henttonen§

* Department of Zoology, Division of Ecology, PO Box 17 (P. Rautatiekatu 13), SF-00014 University of Helsinki, Finland

† Southern Forest Experiment Station, 2500 Shreveport Highway, Pineville, Louisiana 71360, USA

‡ Laboratory of Ecological Zoology, Department of Biology, University of Turku, SF-20500 Turku, Finland

§ Department of Forest Ecology, Finnish Forest Research Unit, PO Box 18, SF-01301 Vantaa, Finland

THE four-year cycle of microtine rodents in boreal and arctic regions was first described in 1924 (ref. 1). Competing hypotheses on the mechanisms underlying the small mammal cycle have been extensively tested^{2–5}, but so far the sustained rodent oscillations are unexplained. Here we use two mutually supportive approaches to investigate this question. First, building on studies of the interaction between rodents and their mustelid predators^{6–9}, we construct a predator–prey model with seasonality. Second, we use a new technique of nonlinear analysis^{10,11} to examine empirical time-series data, and compare them with the model dynamics. The model parameterized with field data predicts dynamics that closely resemble the observed dynamics of boreal rodent populations. Both the predicted and observed dynamics are chaotic, albeit with a statistically significant periodic component. Our results suggest that the multiannual oscillations of rodent populations in Fennoscandia are due to delayed density dependence imposed by mustelid predators, and are chaotic.

As a starting point we use the general predator–prey model¹²

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - \frac{cPN}{N+D} \quad (1)$$

$$\frac{dP}{dt} = vP \left(1 - \frac{qP}{N} \right) \quad (2)$$

where N and P are the prey and predator densities (numbers of individuals per hectare). Numerical responses of both species are logistic, with r and v being the intrinsic growth rates, and K and N/q the 'carrying capacities', respectively. The predator–prey interaction is modelled by a type-2 functional response with parameters c and D .

Seasonality exerts a strong influence on the dynamics of mammals in boreal and arctic regions. We include seasonality in the model as follows. In Fennoscandia, the potential summer breeding season for rodents is about 6 months long¹³, hence we assume equally long summer and winter seasons. During summer, the rodent population breeds continuously, so we use equation (1). Mustelids breed only when prey density exceeds a critical threshold^{14–16}, say N_{crit} . In the model, predator numbers change

Received 30 November 1992; accepted 26 April 1993.

1. May, R. M. *Science* **186**, 645–647 (1974).
2. May, R. M. *Nature* **216**, 459–467 (1976).
3. May, R. M. & Oster, G. F. *Am. Nat.* **110**, 573–599 (1976).
4. Hassell, M. P., Lawton, J. H. & May, R. M. *J. Anim. Ecol.* **45**, 473–486 (1976).
5. Schaffer, W. M. & Kot, M. *Trends Ecol. Evol.* **1**, 58–63 (1986).
6. Nisbet, R. M., Blythe, S. & Gurney, W. S. C. *Trends Ecol. Evol.* **4**, 238–239 (1989).
7. Mani, G. S. *Trends Ecol. Evol.* **4**, 239–240 (1989).
8. Lomnicki, A. *Trends Ecol. Evol.* **4**, 239 (1989).
9. Beryman, A. A. in *Chaos in Ecology* (eds Logan, J. A. & Hain, F. P.) 23–38 (VA Exp. Sta. Inf. Series 91–93, Blacksburg, VA, 1991).
10. Morris, W. F. *Ecology* **71**, 1849–1862 (1990).
11. Beryman, A. A. & Millstein, J. A. *Trends Ecol. Evol.* **4**, 26–28 (1989).
12. Ellner, S. in *Chaos in Ecology* (eds Logan, J. A. & Hain, F. P.) 63–90 (VA Exp. Sta. Inf. Series 91–93, Blacksburg, VA, 1991).
13. Sugihara, G. & May, R. M. *Nature* **344**, 734–741 (1990).
14. Turchin, P. *Nature* **344**, 660–663 (1990).
15. Turchin, P. in *Chaos in Ecology* (eds Logan, J. A. & Hain, F. P.) 39–62 (VA Exp. Sta. Inf. Series 91–93, Blacksburg, VA, 1991).
16. Turchin, P. & Taylor, A. *Ecology* **73**, 289–305 (1992).
17. Logan, J. A. & Allen, J. C. A. *Rev. Ent.* **37**, 455–477 (1992).
18. Tillman, D. & Wedin, D. *Nature* **353**, 653–655 (1991).
19. Casdagli, M. *Physica D* **35**, 335–356 (1989).
20. Ruelle, D. *Proc. R. Soc. Lond. A* **427**, 241–248 (1990).
21. Thomas, W. R., Pomerantz, M. J. & Gilpin, M. E. *Ecology* **61**, 13–17 (1980).
22. Mueller, L. D. & Ayala, F. J. *Ecology* **62**, 1148–1154 (1981).
23. Philippi, T. E., Carpenter, M. P., Case, T. J. & Gilpin, M. E. *Ecology* **68**, 154–159 (1987).
24. Vandermeer, J. *Ecology* **63**, 1167–1168 (1982).
25. Vandermeer, J. *Theor. Pop. Biol.* **22**, 17–27 (1982).
26. Rogers, T. D. *Math. Biosci.* **72**, 13–17 (1984).
27. Milton, J. G. & Belair, J. *Theor. Pop. Biol.* **37**, 273–289 (1990).
28. Pimm, S. L., Jones, J. L. & Diamond, J. *Am. Nat.* **132**, 757–785 (1988).
29. Iwasa, Y. & Roughgarden, J. *Theor. Pop. Biol.* **30**, 194–214 (1986).
30. Roughgarden, J. & Iwasa, Y. *Theor. Pop. Biol.* **29**, 235–261 (1986).
31. Gilpin, M. E. & Hanski, I. *Metapopulation Dynamics: Empirical and Theoretical Investigations* (Academic, London, 1991).
32. Ruelle, D. *Ann. N. Y. Acad. Sci.* **316**, 408–416 (1979).
33. Ricker, W. E. *J. Fish. Res. Bd. Canada* **11**, 559–623 (1954).
34. Collet, P. & Eckmann, J.-P. *Iterated Maps on the Interval as Dynamical Systems* (Birkhäuser, Boston, 1980).
35. Crutchfield, J. P., Farmer, J. D. & Huberman, B. A. *Phys. Rev.* **92**, 45–82 (1982).

according to equation (2) if $N > N_{crit}$, otherwise the predator population declines exponentially, according to

$$\frac{dP}{dt} = d_{high}P \quad (3)$$

With these assumptions, predator growth rate is a function of the prey/predator ratio when densities are high, thus taking into account competitive interactions among the predators¹⁷, but at low densities, predators decline, avoiding a problem in the standard ratio-dependent theory¹⁸.

During winter, food availability for rodents is lower than in summer, as there is no plant growth, the quality of the forage deteriorates, and some foraging sites become inaccessible under snow. We use equation (1) for the rodent population in winter, but with r and K replaced by (the lower values of) r' and K' . These assumptions lead to population growth in winters when the autumn density is low, but to a population decrease in other winters. This is what happens in *Microtus* voles, the key prey species for mustelids^{8,19,20}; *Microtus* typically breed in the winter following the low phase of the rodent cycle^{21,22}. Winter breeding has never been observed in mustelids in Fennoscandia, hence we assume none in the model. But rate of mortality in the predator population is evidently related to prey density. We assume an exponential decline in the predator population during winter, with the rate constant depending on prey density. If $N > N_{crit}$, the rate constant has a value d_{low} , otherwise the same (higher) value d_{high} as in summers when rodents are scarce.

Equations (1) and (2) describe a two-dimensional continuous-time model, which can exhibit only two kinds of qualitative behaviour: a stable equilibrium point or a limit cycle^{7,12}. In the modified version with seasonality, more complex dynamics are possible^{23,24}, and it is easy to pick up parameter values to generate stable dynamics, limit cycles and chaos. The critical question is what kind of dynamics are predicted by parameter values estimated from real data. If the model with field-estimated parameters generates population trajectories that are quantitatively similar to the observed dynamics, then the predation hypothesis explaining microtine oscillations is supported; otherwise it is rejected.

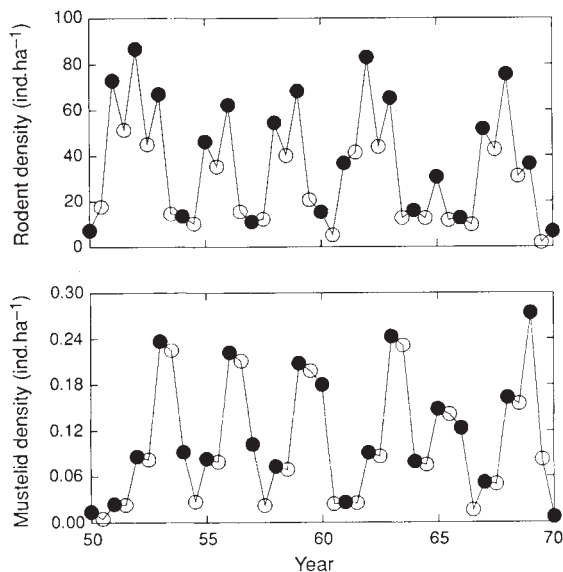


FIG. 1 An example of predicted rodent-mustelid dynamics, generated with the median values of the three parameters that were varied ($q=100$, $D=5$ and $K'=50$; for explanation see Table 1 legend). Upper panel shows changes in rodent density; lower panel, in mustelid density. Open symbols give spring densities, filled symbols autumn densities. The values on the x axis are generations since the beginning of the simulation.

We have estimated the parameter values based primarily on field data collected by E.K. and coworkers in western Finland in 1977-1992 (Table 1). Three parameters are hard to estimate, and we have numerically explored the behaviour of the model for three values of each of the three parameters, a total of 27

TABLE 1 Analysis of model output

q	D	K'	s	T	ACF[T]	LE1	Dynamics
50	5.0	25	0.33	4	0.30	0.60	Chaos
50	5.0	50	0.62	8	0.38	0.59	Chaos
50	5.0	75	0.84	10	0.32	0.39	Chaos*
50	10.0	25	0.04	4/8	0.76/1	-0.58	Limit cycle†
50	10.0	50	0.17	3	0.35	0.31	Chaos
50	10.0	75	0.20	3	0.28	0.44	Chaos
100	5.0	25	0.21	3	0.51	0.05	Chaos‡
100	5.0	50	0.41	5	0.53	0.38	Chaos
100	5.0	75	0.51	6	0.22	0.65	Chaos
100	10.0	25	0.02	4	1	-0.57	Limit cycle
100	10.0	50	0.13	3	1	-0.29	Limit cycle
100	10.0	75	0.11	3	0.99	-0.16	Limit cycle§

Summary of dynamical behaviours of the model with parameter values estimated below. Findings of chaos were confirmed by numerically calculating the dominant Lyapunov exponent²⁵. Variables: q , D and K' are model parameters (described in the text), s is the standard deviation of log-transformed vole densities (a measure of the amplitude), T is the lag at which the autocorrelation function (ACF) reached its peak (a measure of the period), ACF[T] is the value of ACF at that period (an indication of the strength of periodicity), and LE1 is the estimated dominant Lyapunov exponent, which measures sensitivity of dependence on initial conditions (chaos indicated by positive values). Parameter estimation. Parameters were estimated as follows, using data primarily from the Alajoki study area in western Finland, where microtine rodents and their predators have been studied since 1977^{8,26}. r : maximal finite rates of increase from spring to autumn occurred in 1981 ($\times 5.8$), 1984 ($\times 19.5$) and 1990 ($\times 16.4$). We used $r=5.4$ ($= \ln_e [15 \times 15]$; the unit of time is a year); r' : the maximal finite rates of increase from autumn to spring occurred in 1987/88 ($\times 11.8$) and 1990/91 ($\times 2.4$). We assumed $r'=r/2$, thus $r'=2.7$; K : the maximum mean density of *Microtus* voles in fields in Alajoki has been about 100 individuals per hectare (ind. ha^{-1}) in 1977-1990 (ref. 26), hence $K=100$; c : least weasel consumes 0.6 g food per g of body mass per day²⁷. The mean body masses of male and female least weasels are 48 and 35 g, and the body mass of *Microtus* rodents is 25 g (ref. 8). Additionally, a lactating female mustelid consumes three times the amount of food needed by non-lactating females²⁸, and 'surplus killing' may amount to 50% of food requirement²⁹. Based on these values, we estimated $c=600$; D : we are not aware of any data to estimate this parameter, hence we repeated simulations with 3 values that cover the realistic range, $D=2.5, 5$ and 10 (ind. ha^{-1}); v : the maximum finite rate of increase of least weasels occurred in summer 1985, when the density increased from 1.3 ind. km^{-2} in spring, to 5.0 in autumn⁸, which matches the theoretical maximum. Thus $v=2.8$; q : this is another difficult parameter to estimate, and we repeated simulations with 3 values that should cover the range of realistic values, $q=50, 100$ and 200 ; N_{crit} : in 3 years the density of least weasels did not increase in the course of summer, presumably because in these summers the density of rodents was too low to allow breeding by least weasels. The mean spring density of *Microtus* rodents in these years was 2 ind. ha^{-1} . Others have reported substantially higher critical prey densities for breeding by weasels, 10-14 breeding field voles per $\text{ha}^{14,15}$. It is also likely that the value of N_{crit} is related to the value of D . We assumed that $N_{crit}=2D$, thus the N_{crit} values used range from 5 to 20; d_{high} : maximum mortality of least weasels occurred in winter 1989/90, when the autumn density was 5.0 km^{-2} and the spring density was 0.3 (ref. 8). We assumed that $d_{high}=-5$; d_{low} : in 3 of 7 winters the density of least weasels apparently increased from autumn to spring. As there is no evidence for winter breeding by least weasels in Fennoscandia, these increases are probably due to movements of weasels. In any case, when prey is abundant, mortality appears to be very low, and we assumed $d_{low}=-0.1$.

* High-amplitude oscillations similar to dynamics characterizing $D=2.5$.

† 8-point limit cycle sometimes dominated by $T=4$ (ACF[4]=0.76), sometimes by $T=8$ (ACF[8]=1), depending on initial conditions.

‡ For some initial values, dynamics settle onto a 9-point limit cycle.

§ 18-point or 12-point limit cycle dominated by $T=3$.

parameter combinations. We emphasize that all decisions about which values of parameters to include in the numerical explorations of the model were made before we saw the results (parameters estimated by I.H.; model output analysed by P.T.).

Ignoring seasonal variation in numbers, the dynamics predicted by the model range from stability to chaotic oscillations characterized by unrealistically large amplitude (7 orders of magnitude) and long intervals between rodent 'peaks' (> 10 yr). The dynamical extremes are associated with extreme values of the parameters that were varied. Stability was associated with $q=200$, whereas high-amplitude oscillations were associated with $D=2.5$. Excluding parameter combinations involving these values, the model predicts dynamics that are qualitatively similar to the dynamics of boreal Fennoscandian rodents (Table 1). Figure 1 shows the predicted dynamics for the median parameter values, $q=100$, $D=5$ and $K'=50$; Figure 2 gives examples of observed dynamics from Fennoscandia.

A more detailed, quantitative comparison between predicted and observed rodent dynamics was provided by analysing long-term data sets from eight Fennoscandian localities, including the

longest series available (Table 2). The data document fluctuations in the pooled numbers of all microtine rodents at a locality as measured by trapping in the autumn. We calculated the following four quantities: (1) the standard deviation of log-transformed vole densities, s , a measure of the amplitude; (2) the lag at which the autocorrelation function (ACF) reaches its peak, T , a measure of the period of oscillations; (3) the value of ACF at that period, $ACF[T]$, which provides an indication of the strength of periodicity; and (4) the estimated Lyapunov exponent, $LE1$, which measures the sensitivity of dependence on initial conditions, and allows one to distinguish between stable point equilibria and limit cycles ($LE1 < 0$) from chaos ($LE1 > 0$)^{10,11}.

The most striking result arising from these comparisons is that the majority of model-predicted dynamics are chaotic (Table 1), consistent with the results of nonlinear time-series analysis of the real data (Table 2). Only the most southern locality in Table 2 showed non-chaotic, stable dynamics. (This agrees with previous results demonstrating a geographical gradient from high-amplitude, relatively regular oscillations in the north, to low-

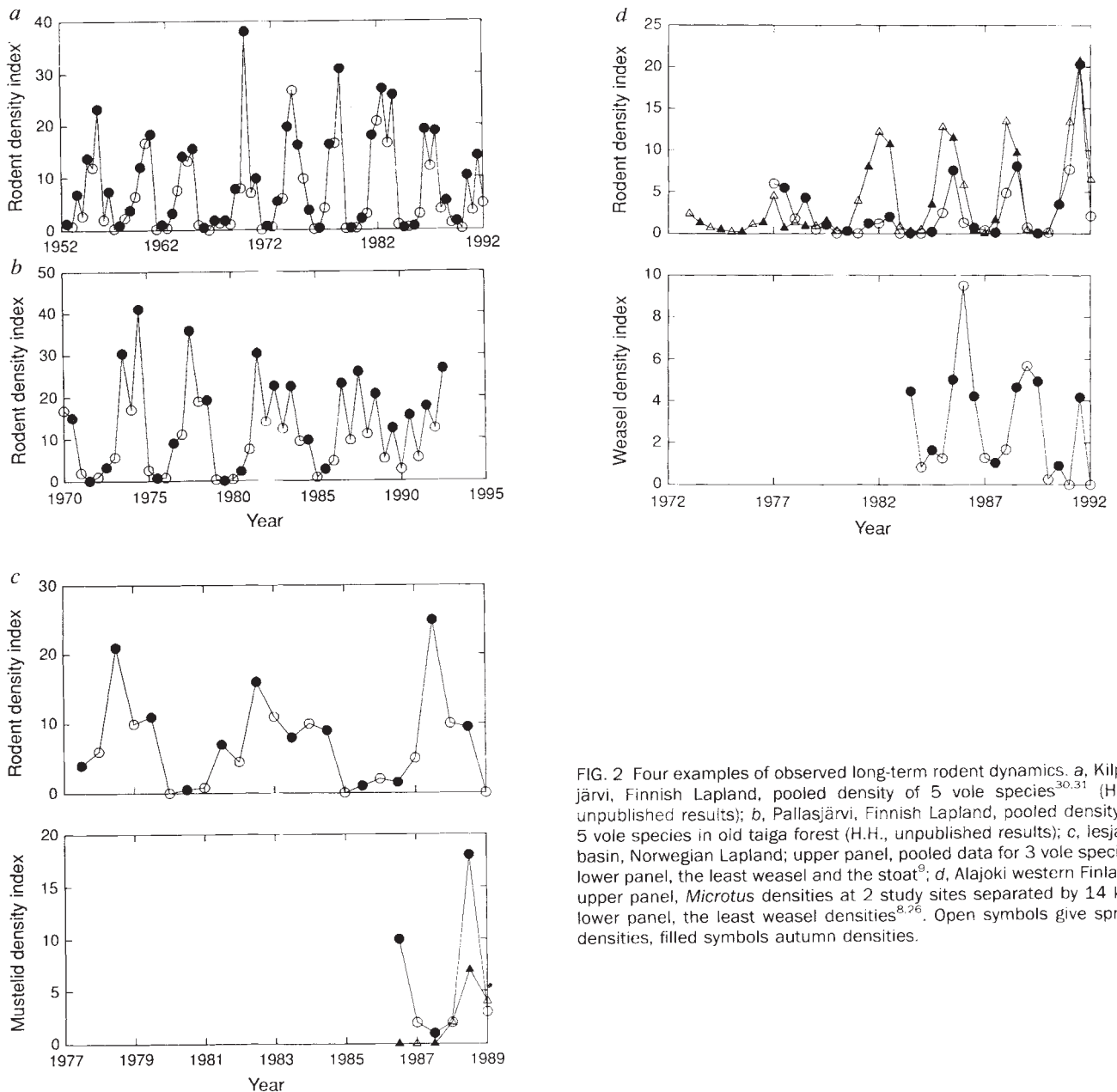


FIG. 2 Four examples of observed long-term rodent dynamics. *a*, Kilpisjärvi, Finnish Lapland, pooled density of 5 vole species^{30,31} (H.H., unpublished results); *b*, Pallasjärvi, Finnish Lapland, pooled density of 5 vole species in old taiga forest (H.H., unpublished results); *c*, Iesjavri basin, Norwegian Lapland; upper panel, pooled data for 3 vole species; lower panel, the least weasel and the stoat⁹; *d*, Alajoki western Finland; upper panel, *Microtus* densities at 2 study sites separated by 14 km; lower panel, the least weasel densities^{8,26}. Open symbols give spring densities, filled symbols autumn densities.

TABLE 2 Analysis of vole time series

Locality	Latitude	Years	s	T	ACF[T]	LE1
Kilpisjärvi*	69°	1949–1970	0.58	5	0.24	0.12
Kilpisjärvi*	69°	1971–1992	0.68	5	0.44	0.12
Pallasjärvi	68°	1970–1992	0.73	4	0.41	1.36
Kola	67°	1946–1964	0.79	4	0.09	0.70
Umeå	64°	1971–1988	0.55	4	0.49	0.08
Sotkamo	64°	1966–1992	0.49	4	0.51	0.21
Ruotsala	63°	1973–1992	0.65	3	0.61	0.87
Alajoki	63°	1977–1992	0.77	3	0.41	1.63
Loppi	61°	1972–1992	0.27	—	—	-2.06

* Kilpisjärvi data were analysed in two separate pieces to compensate for non-stationarity in this long data set. Variables: s, T, ACF[T] and LE1 as in Table 1.

amplitude, irregular oscillations in the south⁴, probably reflecting the stabilizing effect of abundant generalist predators in the south⁷.) Despite being chaotic, model-predicted oscillations were characterized by statistical periodicities, with a typical period of 3 to 5 yr, although for some more extreme parameter combinations the predicted period was longer. These periodicities were rather weak in strength, with ACF[T] varying from 0.2 to 0.5. The observed oscillations were also characterized by periodicities of 3 to 5 yr, and their strength varied from 0.1 to 0.6. The amplitude of the observed vole fluctuations was somewhat greater than the amplitude predicted by the model. This is not unexpected, because the model does not include stochasticity, which would tend to increase the amplitude. According to these quantitative measures, the dynamics predicted by the model with median values of parameters lie squarely in the middle of the observed spectrum of dynamics.

Figure 2 gives the best-documented empirical data from four Fennoscandian localities. We draw attention to apparent long-term changes in the type of dynamics at two of the four localities. At Pallasjärvi, Finnish Lapland (Fig. 2b), the multiannual cyclic component was evident until the mid-1980s, but has been absent since that time. This change in the pattern of dynamics has been associated with the practical absence of the field vole *Microtus agrestis* and the least weasel *Mustela nivalis* from the study area⁶ (H.H., unpublished results). It is not clear why these species have become regionally extinct or very scarce, but the lack of multiannual oscillations in the absence of these two key species is consistent with the idea that the relatively regular oscillations are maintained by their interaction¹⁶, and become reflected in the dynamics of the other small mammal species because of shared predators^{6,16}. In Alajoki, western Finland, four distinct 3-yr cycles have been observed since 1984, but in 1973–1983, rodent density was constantly low (Fig. 2d). Although such irregularities could be expected as a part of strongly chaotic dynamics, here they are more likely to reflect subtle changes in the relative abundances of the various species in the small mammal and predator communities, induced for example by changes in the landscape structure. Our modelling results indicate that biologically plausible adjustments in parameter values may push the dynamics from annual cycles (multiannual stability) to multiannual cycles with long period and high amplitude.

Our results add a critical piece to the growing evidence that the 3–5 yr small mammal cycle in Fennoscandia and probably elsewhere is generated by delayed density dependence as a result of specialist predators. No other hypothesis about the rodent dynamics has been formulated as a quantitative model and been successfully tested with field data. □

- Batzli, G. O. in *Wildlife 2001: Populations* (eds McCullough, D. M. & Barrett, R. H.) 831–850 (Elsevier, 1992).
- Henttonen, H., Oksanen, T., Jortikka, A. & Haukiala, V. *Oikos* **50**, 353–365 (1987).
- Hanski, I., Hansson, L. & Henttonen, H. *J. Anim. Ecol.* **60**, 353–367 (1991).
- Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. *Oecologia* **88**, 552–561 (1991).
- Oksanen, L. & Oksanen, T. *Ecography* **15**, 226–236 (1992).
- Turchin, P. *Oikos* (in the press).
- Turchin, P. & Millstein, J. A. *EcoDyn/RSM: Response Surface Modelling of Nonlinear Ecological Dynamics* (Applied Biomathematics, Setauket, NY, 1993).
- May, R. M. *Complexity and Stability of Model Ecosystems* (Princeton Univ. Press, NJ, 1973).
- Hansson, L. & Henttonen, H. *Ann. Zool. Fennici*, **22**, 277–288 (1985).
- Erlinge, S. *Oikos* **25**, 308–314 (1974).
- Tapper, S. *J. Anim. Ecol.* **48**, 603–617 (1979).
- Henttonen, H. *Oikos* **50**, 366–370 (1987).
- Korpimäki, E. & Norrdahl, K. *Oikos*, **55**, 205–215 (1989).
- Hanski, I. *Trends Ecol. Evol.* **6**, 141–142 (1991).
- Erlinge, S. *Oikos* **26**, 378–384 (1975).
- Tapper, S. *C. J. Zool.* **179**, 219–224 (1976).
- Hansson, L. in *Winter Ecology of Small Mammals* (ed. Merritt J. F.) 225–234 (Spec. Publ. Carnegie Mus. Nat. Hist. No. 10, Pittsburgh, 1984).
- Kaikusalo, A. & Tast, J. in *Winter Ecology of Small Mammals* (ed. Merritt J. F.) 243–252 (Spec. Publ. Carnegie Mus. Nat. Hist. No. 10, Pittsburgh, 1984).
- May, R. M. *Science* **186**, 645–647 (1974).
- May, R. M. *Nature* **261**, 459–467 (1976).
- Wolff, A., Swift, J. B., Swinney, H. L. & Vastano, J. A. *Physica* **16D**, 285–317 (1985).
- Korpimäki, E. & Norrdahl, K. *Oikos* **62**, 195–208 (1991).
- Gillingham, B. J. *J. Mammal.* **65**, 517–519 (1984).
- Erlinge, S. et al. *Oikos* **40**, 36–52 (1983).
- Jedrzejska, B. & Jedrzejski, W. *Acta Theriol.* **34**, 347–359 (1989).
- Laine, K. & Henttonen, H. *Oikos* **40**, 407–418 (1983).
- Laine, K. & Henttonen, H. *Oikos*, **50**, 389–395 (1987).

ACKNOWLEDGEMENTS. We thank A. Berryman, M. Gyllenberg, R. May, H. Metz, K. Norrdahl and C. Thomas for discussion and for comments on the manuscript.

Unilateral neglect restricted to visual imagery

C. Guariglia*†, A. Padovani‡, P. Pantano‡ & L. Pizzamiglio*†§

Departments of *Psychology and †Neurology, University of Rome 'La Sapienza', Via dei Marsi 78, 00185 Rome, Italy
‡ Clinica S. Lucia, Via Ardeatina 306, 00179 Rome, Italy

DISORDERS in perceiving and exploring the visual space contralateral to a brain lesion have been frequently described. Many patients with hemi-neglect for extrapersonal space also show neglect in a representational domain when the task requires imagining a well-known piazza from a given vantage point^{1,2} or comparing two visual images^{3–5}. Cognitive⁶ and psychophysiological⁷ studies show a functional parallelism between the perceptual and imaginative domain⁷, indicating that spatial perception and imagery share the same neural substrata. Here we describe a patient with a persistent disorder in visual imagery for familiar piazzas in the absence of any neglect for stimuli located in a far⁸ or near⁹ space or on his own body¹⁰. Contrary to previous cases involving imagery disorders, computerized tomography scans showed a lesion confined to the right frontal lobe, suggesting the role of the frontal lobe in some specific types of mental imagery.

A 59-year-old right-handed man was examined 16 months after an ischaemic stroke, which produced a left hemiparesis. A computerized tomography (CT) scan showed a large lesion involving the right frontal and anterior temporal lobe (Fig. 1). A SPECT study showed a hypoperfusion in the lesioned frontal area, but not a perfusional deficit remote from the infarct, except in the contralateral cerebellum. A neuropsychological examination showed no mental deterioration or visual field defects, some difficulty in abstract reasoning and face recognition, and a mild impairment in selective attention and in constructional apraxia (Table 1).

The patient's performances on tests for visuo-spatial (Line and Letter Cancellation, Wundt–Jastrow Area Illusion and Sentence Reading) and personal neglect¹¹ were normal. In contrast, when

§ To whom correspondence should be addressed.

Received 22 March; accepted 27 April 1993.

- Elton, C. *Voles, Mice and Lemmings: Problems in Population Dynamics* (Oxford Univ. Press, 1942).
- Krebs, C. J. & Myers, J. H. *Adv. ecol. Res.* **8**, 267–399 (1974).
- Christian, C. J. in *Populations of Small Mammals under Natural Conditions* (ed. Snyder, D. P.) 143–158 (Pymatuning Lab. Ecol. Spec. Publ. 5, 1978).
- Hansson, L. & Henttonen, H. *Trends Ecol. Evol.* **3**, 195–200 (1988).