

13. Brooks, C. R. & Bogni, F. *Mater. Character.* **38**, 103–117 (1997).
 14. Steele, A. et al. *Lunar Planet. Sci.* **28**, 1369–1370 (1997).
 15. Morrison, D. A. & Clanton, U. S. *Proc. Lunar Planet. Sci. Conf.* **10**, 1649–1663 (1979).
 16. Newbury, D. E., Joy, D. C., Echlin, P., Fiori, C. E. & Goldstein, J. I. in *Advanced Scanning Electron Microscopy and X-Ray Microanalysis* (Plenum, New York, 1986).
 17. Kajander, E. O., Kuronen, I., Åkerman, K., Pelttari, A. & Çiftçioğlu, N. in *Proc. Soc. Photo-Opt. Instrum. Eng.* Vol. 3111 (ed. Hoover, R. B.) 420–428 (Int. Soc. Opt. Eng., Bellingham, WA 1997).
 18. Çiftçioğlu, N., Pelttari, A. & Kajander, E. O. in *Proc. Soc. Photo-Opt. Instrum. Eng.* Vol. 3111 (ed. Hoover, R. B.) 429–435 (Int. Soc. Opt. Eng., Bellingham, WA 1997).
 19. Kieft T. L. in *Nonculturable Microorganisms in the Environment* (eds Colwell, R. R. & Grimes, D. J.) (Chapman and Hall, New York, in the press).
 20. Romanek, C. S. et al. *Nature* **372**, 655–657 (1994).
 21. Valley, J. W. et al. *Science* **275**, 1633–1638 (1997).
 22. Gleason, J. D., Kring, D. A., Hill, D. H. & Boynton, W. V. *Geochim. Cosmochim. Acta* **61**, 3503–3512 (1997).
 23. Hanzlik M., Winkhofer M. & Petersen N. *Earth Planet. Sci. Lett.* **145**, 125–134 (1996).
 24. von Dobeneck T., Petersen N. & Vali H. *Geowiss. Uns. Zeit* **1**, 27–35 (1987).
 25. Westall, F. in *Astronomical and Biochemical Origins and the Search for Life in the Universe* (eds Cosmovici, C.B., Bowyer, S. & Werthimer, D.) 491–504 (Compositori Editrice, Bologna, 1997).
 26. Westall F. *Darmstädter Beiträge zur Naturges.* **4**, 29–43 (1994).

Travelling waves in vole population dynamics

Spatial self-organization patterns in population dynamics have been anticipated^{1–3}, but demonstrating their existence requires sampling over long periods of time at a range of sites. Voles cause severe economic damage and are therefore extensively

monitored, providing a source of the required data. Using two long-term data sets^{4–6} we now report the existence of travelling waves in vole population numbers.

Information about the intensity of annual vole damage to young forests was available for the years 1972–83 for 19 forestry board districts of Finland^{5,6}. The geographical distribution of the most damaged areas fluctuates (Fig. 1a, b) and the timing of damage is asynchronous among the different areas. Locally, the damage peaks at intervals of three to four years, matching the cyclic dynamics of Scandinavian voles⁷. This is in agreement with simulation studies² showing that spatial order is associated with the presence of spatial waves showing a certain degree of periodicity.

Correlation between the latitude of the ‘centre of mass’ and the annual severity of the damage (Fig. 1a, b) is $r=0.84$ ($P<0.001$; for the longitude $r=0.13$). Thus, with increasing volume of vole damage the damage epicentre moves north. There was also a negative correlation between intensity of damage and distance between provinces ($r=-0.47$; $P<0.001$) suggesting that nearby localities have similar damage levels, and providing another indication of spatial structure⁸ in vole damage.

We also analysed records of vole plagues in 53 departments of France for the years 1900–35¹ (Fig. 1c, d). There were rapid changes in the extent of the plagued area, but there were no clear periodicities

like those seen in the Scandinavian voles⁷. Again there was a correlation between the latitude of the annual location of the centre of mass and the geographical extent of the damage ($r=-0.67$, $P<0.001$; for the longitude $r=0.06$). Accordingly, the French vole plagues spread from north to south, whereas in Finland they spread from south to north.

A variable is said to be spatially autocorrelated when it is possible to predict the values of this variable in one site from the known values at nearby sampling sites⁹. We performed autocorrelation analyses for irregularly spaced interval (Finland) or nominal scales (France)¹⁰.

For the Finnish data, we computed annual autocorrelation coefficients^{9–11} for the distance class of 200 km assuming binary links. We detected significant positive spatial autocorrelation in six of the twelve years. For the French data we computed annual spatial autocorrelations using binary weights and assuming a link between sites that were less than 120 km apart. We found a significant spatial autocorrelation present in the data in 14 of the 33 years. Both results indicate that spatial structure exists in these populations.

By identifying spatial autocorrelation in vole populations and an annually moving epicentre of vole plagues as a function of damage extent, we conclude that travelling waves, or pulses, in the dynamics of vole populations exist, a phenomenon predicted^{1–3} by theoretical population ecology.

Esa Ranta

Department of Ecology and Systematics,
 University of Helsinki,
 PO Box 17,
 FIN-00014 Helsinki,
 Finland
 e-mail: esa.ranta@helsinki.fi

Veijo Kaitala

Department of Biological and Environmental
 Science,
 University of Jyväskylä,
 Box 35,
 FIN-40351 Jyväskylä,
 Finland

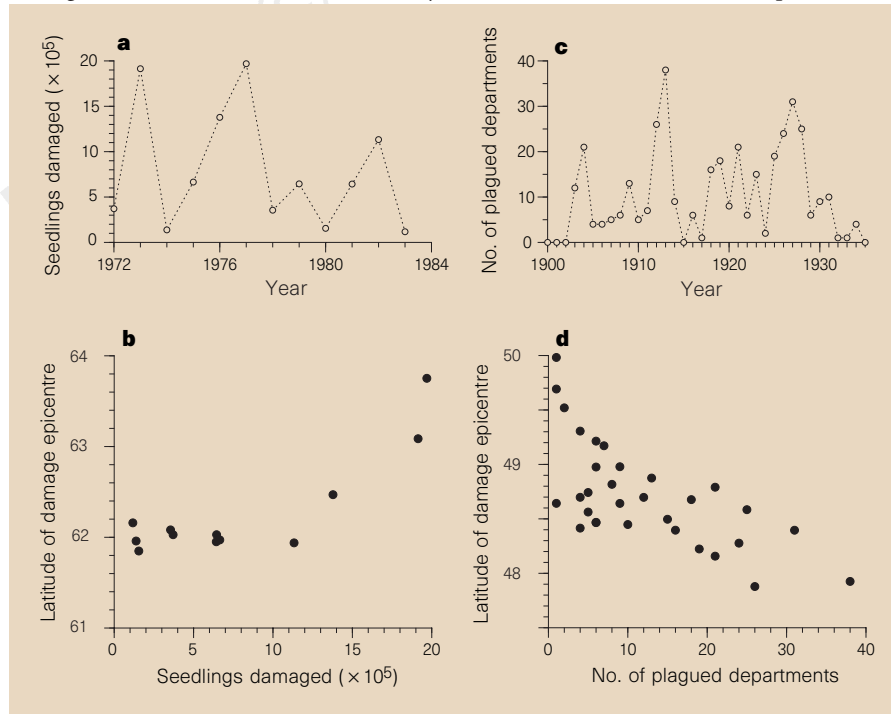


Figure 1 Extent and severity of vole damage. **a**, The number of seedlings destroyed by voles on study plots in young forest plantations in Finland^{5,6}. **b**, The dynamics are characterized by movement of the annual damage epicentre from south to north as total damage increases. **c**, Geographical extent of French⁴ vole plagues; and **d**, annual epicentre of plagues plotted against the number of plagued departments.

1. Hassell, M. P., Comins, H. N. & May, R. M. *Nature* **353**, 255–258 (1991).
 2. Rohani, P. & Miramontes, O. *Proc. R. Soc. Lond. B* **260**, 335–342 (1995).
 3. Bascompte, J. & Sole, R. *Trends Ecol. Evol.* **10**, 361–366 (1995).
 4. Elton, C. *Voles, Mice and Lemmings. Problems in Population Dynamics* (Clarendon, Oxford, 1942).
 5. Teivainen, T. *Folia Forestalia* **387**, 1–23 (1979).
 6. Teivainen, T. *Metsäntutkimuslaitoksen Tiedonantaja* **145**, 1–12 (1984).
 7. Hansson, L. & Henttonen, H. *Oecologia* **67**, 394–402 (1985).
 8. Ranta, E., Kaitala, V., Lindström, J. & Lindén, H. *Proc. R. Soc. Lond. B* **262**, 113–118 (1995).
 9. Sokal, R. R. & Oden, F. M. L. S. *Biol. J. Linn. Soc.* **10**, 199–228 (1978).
 10. Legendre, P. & Fortin, M.-J. *Vegetatio* **80**, 107–138 (1989).
 11. Moran, P. A. P. *Biometrika* **37**, 17–23 (1950).