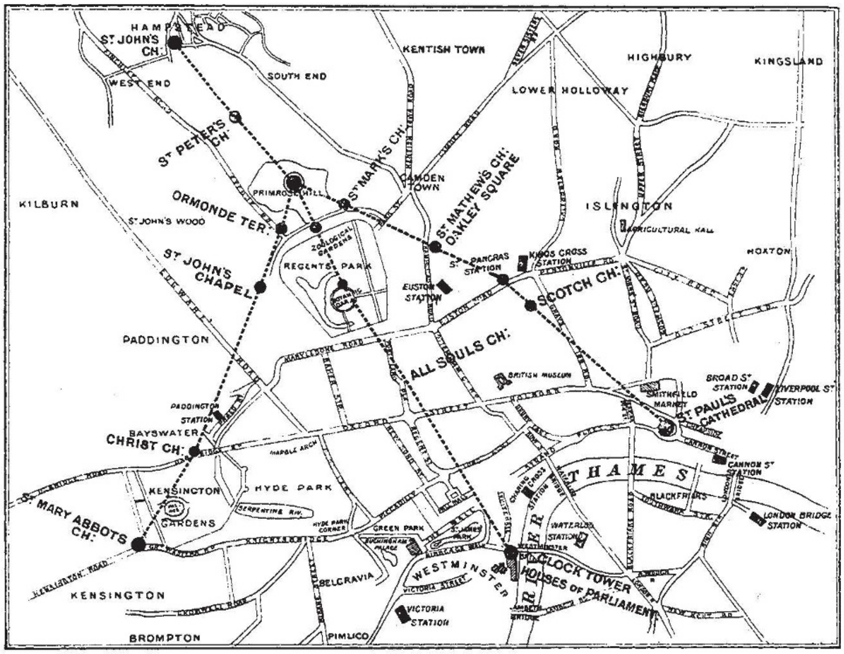
100 years ago THE DARKNESS OF LONDON AIR



THE constitution of London fogs has been carefully gone into by several well-known men of science; and the results obtained are of very great interest, as they prove, amongst other things, that during the winter London air has an unusually large amount of carbonic acid in it. Various observations were taken in London during the winter of 1887–88. During the five months selected, Christ Church, Lancaster Gate, and St. Mary Abbot's Church, Kensington, on the south-west line; the Clock Tower, Houses of Parliament, on the south line, and the Scotch Church, Regent's Square; and St. Paul's Cathedral, on the south-east line, were *never once* seen. When it is known that on any fine day during the late spring, summer, and early autumn, you can see right across London, on any one of the selected lines, it will be easy to realize how thick the air over London is during the winter. From *Nature* **39**, 442; 7 March 1889.

much less in the real world.

In his new paper[8], Mountford has extended this discussion. Hassell assumed that the competitive effects determining larval survival are 'scramble': when resources are abundant, all do well, and when resources are sparse, all do badly. The result can be a highly nonlinear, 'boom-and-bust' relation, which can fairly easily produce oscillatory or chaotic dynamics. Mountford, on the other hand, bases all his simulations on density-dependent relations corresponding to 'contest' competition, which assumes resources are distributed in a hierarchical fashion, so that a few individuals do well even in hard times. These smooth relations chosen by Mountford to characterize larval competition can never generate oscillatory, much less chaotic, dynamics. With his pseudo-data generated in this way, Mountford finds that conventional methods can easily detect the density-dependent effects, with spatial heterogeneity and environmental noise presenting no difficulties.

The problems discovered by Hassell seem to me to depend largely on the interplay between what might be called 'density-dependent noise' (generated by nonlinear relations that, in some patches in a fluctuating environment, can be severe enough to produce chaos) and 'density-independent noise' (generated directly by environmental stochasticity), in a patchy world[13]. So I am not surprised that these problems do not arise in systems such as Mountford's, where the nonlinearities are too weak to produce oscillations or chaos. It is perhaps unfortunate that Mountford does not mention this qualitative difference between his chosen density-dependent functions and the boom-and-busty ones of Hassell; the differences between Hassell's and Mountford's simulations seem puzzling if this underlying difference is not appreciated.

This being said, Mountford's study is interesting in several ways. First, it is useful to have an explicit indication that patchiness and stochastic effects, by themselves, are insufficient to upset traditional methods of data analysis. Severe nonlinearities in density-dependent effects thus seem to be an essential ingredient in such problems as may exist. Second, Mountford shows that (in the absence of strong nonlinearities) spatial heterogeneity can actually enhance our ability to detect density dependence: "if there are a number of sets of population density series all with the same mean and the same variability but with differing degrees of spatial heterogeneity, then the detection of density dependence improves with increasing spatial heterogeneity". Third, the pronounced differences between Hassell's studies (based on 'scramble' competition, with its potential for strong nonlinearities and chaotic dynamics) and Mountford's (based on 'contest' competition) highlight the often-neglected way in which the behaviour of individuals influences the dynamics of populations. Indeed, Lomnicki's recent book[14] is devoted to showing explicitly how some kinds of foraging (or other) behaviour result in 'scrambling' competitive relations and thus in highly volatile dynamics for the population, while different kinds of individual behaviour result in 'contest' competition and thus in tame dynamics. The comparison between Hassell's and Mountford's papers provides another perspective on Lomnicki's basic theme.

There seems to me to be much scope for further studies of ways in which spatial heterogeneity, environmental unpredictability, and nonlinear interactions within and between populations can swirl together to confound empirical studies aimed at understanding what prevents the long-term average density of a population from increasing indefinitely (or decreasing to zero in a time short compared with average extinction times). Using computers to generate pseudo-data for imaginary worlds whose rules are known, and then testing conventional methods of data analysis for their efficiency in revealing these known rules, seems to me to be a useful approach. We must all, of course, join Mountford in agreeing with Dempster and Pollard[15] that "the best hope of unravelling the roles of different factors in the population dynamics of animals, still rests in analysis of long-term, life-table data". The worry remains that, until we have a surer grasp of possible complications in the analysis, we cannot be certain we have gathered the appropriate data, no matter how long and carefully we have toiled in the field. □

Robert M. May is a Royal Society Research Professor at Imperial College London and at the Department of Zoology, University of Oxford, Oxford OX1 3PS, UK.

1. Gleick, J. *Chaos: Making a New Science* (Viking, New York, 1987).
2. Lorenz, E.N. *J. atmos. Sci.* **20**, 130–141 (1963).
3. Li, T.Y. & Yorke, J.A. *Amer. Math. Mth.* **82**, 732–733 (1975).
4. May, R.M. *Science* **186**, 645–647 (1974).
5. May, R.M. & Oster, G.F. *Am. Nat.* **110**, 573–599 (1976).
6. Schaffer, W.M. & Kot, M. *Trends Ecol. Evol.* **1**, 58–63 (1986).
7. Berryman, A.A. & Millstein, J.A. *Trends Ecol. Evol.* **4**, 26–28 (1989).
8. Mountford, M.D. *J. anim. Ecol.* **57**, 845–858 (1988).
9. Hassell, M.P. *J. anim. Ecol.* **56**, 705–713 (1987).
10. Colwell, R.K. & Winkler, D.W. in *Ecological Communities: Conceptual Issues and the Evidence* (eds Strong, D.R., Simberloff, D., Abele, L.G. & Thistle, A.B.) 344–359 (Princeton University Press, 1984).
11. Harvey, P.H. & May, R.M. *Nature* **314**, 228–229 (1985).
12. Hassell, M.P., Southwood, T.R.E. & Reader, P.M. *J. anim. Ecol.* **56**, 283–300 (1987).
13. May, R.M. *Proc. R. Soc. B* **228**, 241–266 (1986).
14. Lomnicki, A. *Population Ecology of Individuals* (Princeton University Press, 1988).
15. Dempster, J.P. & Pollard, E. *Oikos* **46**, 4413 (1986).