



THE UNIVERSITY OF CHICAGO PRESS JOURNALS

Nonlinear Dynamics and Population Disappearances

Author(s): Kevin McCann and Peter Yodzis

Source: *The American Naturalist*, Vol. 144, No. 5 (Nov., 1994), pp. 873-879

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: <https://www.jstor.org/stable/2463019>

Accessed: 27-09-2018 19:24 UTC

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



JSTOR

The American Society of Naturalists, The University of Chicago Press are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*

NONLINEAR DYNAMICS AND POPULATION DISAPPEARANCES

Local extinctions generally have been attributed to demographic stochasticity (requiring very small population sizes) or to extrinsic effects such as environmental stochasticity. It is shown here that, without any of these factors, the presence of chaotic transients in very simple and plausible ecosystem models can produce sudden and unforeseeable disappearances of populations (fig. 1). The mathematical background and the ecological context for these occurrences are discussed.

Figure 1 is a time series for the top predator in a simple three-species food chain; specifically it is a solution of the equations

$$\begin{aligned}\frac{dR}{dt} &= R \left(1 - \frac{R}{K} \right) - \frac{x_C y_C C R}{R + R_0}, \\ \frac{dC}{dt} &= x_C C \left(-1 + \frac{y_C R}{R + R_0} \right) - \frac{x_P y_P P C}{C + C_0},\end{aligned}$$

and

$$\frac{dP}{dt} = x_P P \left(-1 + \frac{y_P C}{C + C_0} \right),$$

where R is resource density, C is consumer density, and P is predator density, while K (the resource carrying capacity), x_C , y_C , x_P , y_P , R_0 , and C_0 are positive constants. A previous article (Yodzis and Innes 1992) shows how the other parameters can be derived from bioenergetics. The parameters $x_C = 0.4$, $y_C = 2.009$, $x_P = 0.08$, and $y_P = 2.876$ were chosen so that both consumer and predator could be either invertebrate or vertebrate ectotherms, with a reasonable predator:prey (= consumer) body mass ratio. The choices $R_0 = 0.16129$ and $C_0 = 0.5$ are more or less arbitrary, and the value chosen for K (= 1) is related to figure 2 as discussed below.

Units of time have been chosen in which the resource intrinsic growth rate is one, so time here could be anything from days to years. Even if the resource grows rapidly, so that time is measured in days, figure 1 reveals a startling behavior. The density varies in a chaotic fashion but, for a very long time, rather tamely: it remains within a nicely bounded range. Then, without any warning, the density drops rapidly to zero. We will call this behavior a *population disappearance*. It is a chaotic transient, associated with a crisis, also termed a *chaotic blue sky catastrophe* (Rössler 1976; Grebogi et al. 1983; Abraham and Stewart 1986; Thompson and Stewart 1986). Chaotic transients have also been reported

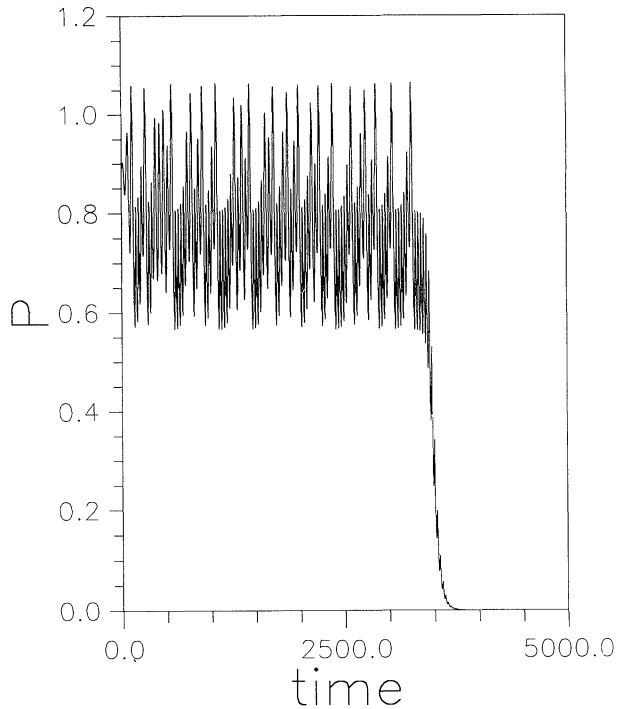


FIG. 1.—Predator density P as a function of time, for the equations and parameter values stated in the text.

in discrete-time predator-prey models (Haderler and Gerstmann 1990; Neubert and Kot 1992) and in epidemiology (Engbert and Drepper 1994).

Of course, population crashes and local extinctions have been observed in many ecological systems. Generally they are attributed to demographic stochasticity, environmental stochasticity, or extrinsic pushes from one basin of attraction to another (Soulé 1987; Harrison 1991). In our example, none of these things are present. There is no stochasticity of any kind, and the final disappearance of the population is not triggered by any extrinsic influence, nor is it anticipated by any sign in terms of the behavior of the population densities. For reasons that we will state below, disappearances of this sort (or sudden unanticipated jumps to some other attractor) ought to be quite common in ecosystem models with realistic, nonlinear functional responses, in productive environments.

The above system of equations is known to possess chaotic solutions (Hastings and Powell 1991), but it has a still richer bifurcation structure, and consequent repertory of qualitative behaviors, than this. Some of it can be seen in figure 2, where the resource carrying capacity K is allowed to vary. Up to $K = 0.997$ we see a period doubling route to chaos. However, this is all going on within one basin of attraction. The system has another attractor, which is a cycle in the R - C

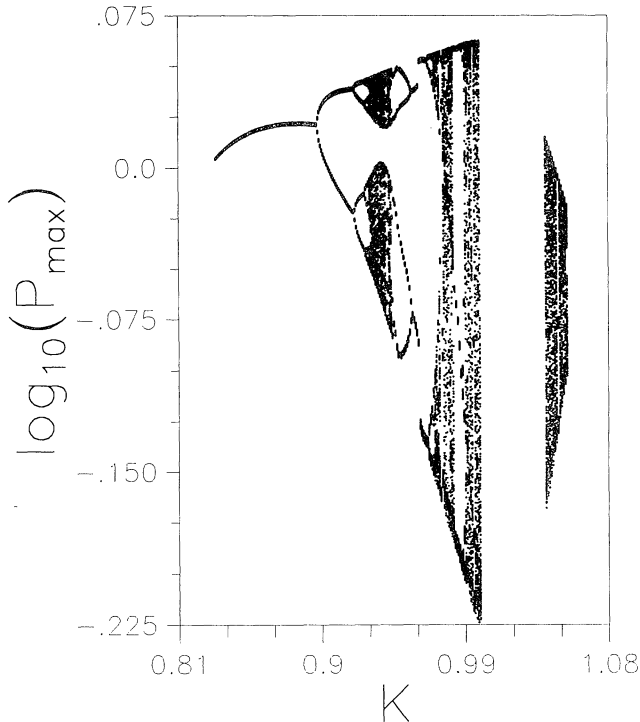


FIG. 2.—Bifurcation diagram as the carrying capacity K is varied

plane (top predator absent). The boundary between the two basins is the inset of a saddle cycle. (Near the crisis this boundary is very likely a complicated fractal set.) At $K = 0.997$, the basin boundary “collides” with the chaotic attractor (as discussed in the next paragraph)—this is the crisis or blue sky catastrophe—and at somewhat higher K values there is only one attractor in the system, namely the cycle in the R - C plane. Figure 3 shows phase space trajectories before (fig. 3A) and after (fig. 3B) the crisis. At $K = 1.039$ there is a similar (but reversed) crisis, in which two basins of attraction reappear, then another crisis at $K = 1.053$, back to one basin of attraction at $P = 0$.

It is generally believed that a crisis in this sense always involves a global bifurcation, specifically a homoclinic or heteroclinic event. We conjecture that, in our case, for K values just below the crisis value, a branch of the outset of the saddle cycle asymptotically approaches the chaotic attractor, while in a Poincaré section the inset of the saddle cycle comes near the attractor. Then at the critical value of K the outset branch is identical to the chaotic attractor and the inset has points of tangency with that set. This generates an extremely complex geometry known as a homoclinic tangle (Guckenheimer and Holmes 1983). (The discontinuity at $K = 0.958$ in fig. 2 is another global bifurcation known as an explosion [Ueda 1980; Rössler 1976].)

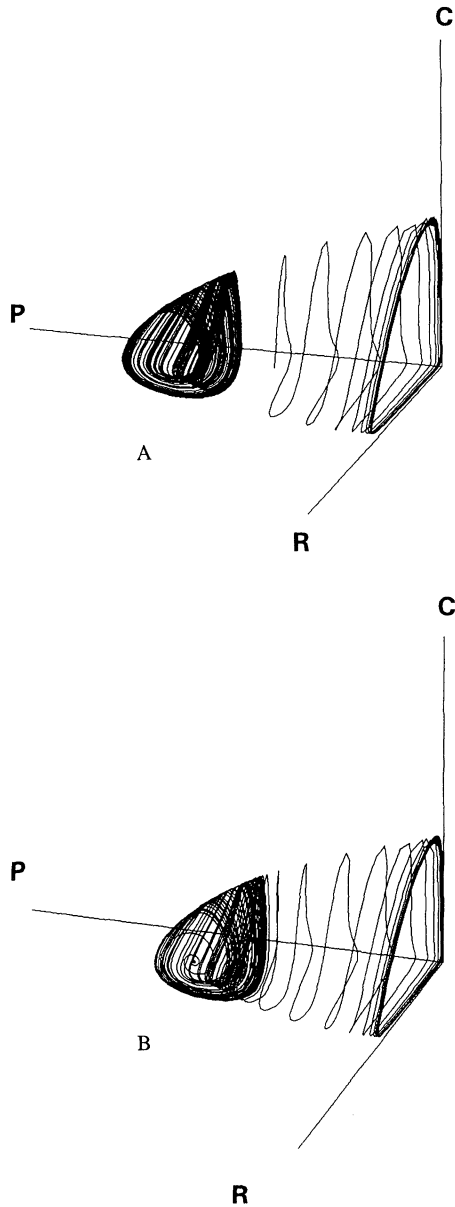


FIG. 3.—Phase space trajectories for (A) $K = 0.99$ and (B) $K = 1.00$. In A two different initial values for P are used ($P = 0.3, 0.45$) to display the two basins of attraction. In B there is only one attractor, a cycle in the R - C plane.

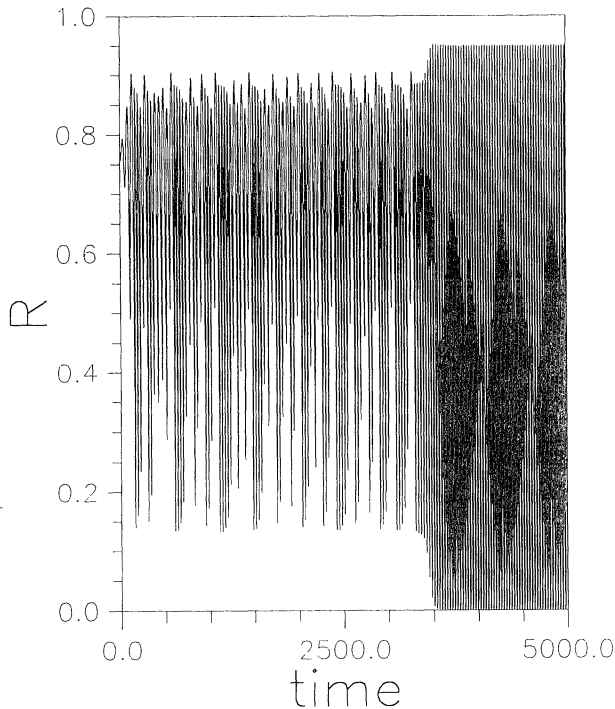


FIG. 4.—Resource density R as a function of time, for the equations and parameter values stated in the text, with the same initial densities as fig. 1.

After the crisis, there is no longer a chaotic attractor, but there is a strong vestige of that set, as revealed in chaotic transients such as figure 1. Putting it somewhat crudely, one can think of the crisis as opening up a “hole” in the (former) attractor, out of which trajectories flow to the R - C plane. Depending on exactly where on the former chaotic attractor a trajectory originates, it may take a very long time to find its way to the hole, after which it will rapidly approach the R - C plane. Because of the chaotic geometry of trajectories near the former attractor, the time until disappearance as a function of initial population density varies in a seemingly random fashion. This could be used as a diagnostic in lab experiments to distinguish population disappearances in our sense from other causes of local extinction, which imply decreasing times to extinction as population density increases (Soulé 1987; Harrison 1991).

All of these complex dynamical behaviors are produced by the presence within the system of oscillations (due to pairwise predator-prey interactions) with incommensurate frequencies, which are coupled through the food web. While a formal sensitivity analysis with respect to parameters is impracticable here, because of this mechanism we expect the occurrence of chaos and of chaotic transients to be robust, both with respect to parameter variation in our system (with support from fragmentary numerical experimentation) and with respect to the forms of multispecies models generally. In more complex food webs one or more species

might be lost in a crisis, or there might be no species lost. As well, one might have cascades of crises, each one set up by the previous crisis. There may also be further collapses precipitated by demographic stochasticity. For instance, in our example the presence of the top predator tends to damp the consumer-resource oscillations, and after the top predator disappears the resource enters a regime of extreme oscillations (fig. 4).

The general picture of ecosystem behavior that emerges is one of unforeseen, indeed unforeseeable, jumps from one configuration to another, on a wide range of timescales, often involving local extinctions (which might, however, be reversed by colonization events). There is a basic ecological requisite for an ecosystem to reside in this region of parameter space, namely, high primary productivity. Figure 1 displays this property with respect to the carrying capacity K ; similar behavior emerges if we increase the turnover rate of the resource. However, relative turnover rates are constrained by predator-prey body mass ratios and their implications for dynamical rates (Yodzis and Innes 1992), so K is the freer parameter.

One thinks of highly enriched systems, such as agroecosystems or fish farms, or perhaps attempts to create artificial ecosystems. But we emphasize that "high productivity," in the appropriate sense of "large K ," is measured relative to the saturation constants R_0 and C_0 of the consumer and predator functional responses, that is, relative to the feeding biology of the particular animals in the system. High productivity in this sense may differ from high productivity in a strictly energetic sense. So answering the question where one expects to see this sort of behavior is actually quite complicated. From the standpoint of dynamics, consumer functional responses under field conditions are a crucial, if difficult to measure, class of data.

ACKNOWLEDGMENTS

We thank J. Ball, J. Fryxell, M. Gilpin, W. Langford, T. Nudds, and R. Schneider for discussions, and the Natural Sciences and Engineering Research Council of Canada for financial support.

LITERATURE CITED

- Abraham, R. H., and H. B. Stewart. 1986. A chaotic blue sky catastrophe in forced relaxation oscillations. *Physica* 21D:394–400.
- Engbert, R., and F. R. Drepper. 1994. Qualitative analysis of unpredictability: a case study from childhood epidemics. In A. V. Holden, ed. *Proceedings in Nonlinear Science*. Wiley, New York (in press).
- Grebogi, C., E. Ott, and J. A. Yorke. 1983. Crises, sudden changes in chaotic attractors, and transient chaos. *Physica* 7D:181–200.
- Guckenheimer, J., and P. Holmes. 1983. *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*. Springer, Berlin.
- Hadeler, K. P., and I. Gerstmann. 1990. The discrete Rosenzweig model. *Mathematical Biosciences* 98:49–72.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Pages

- 73–88 in M. Gilpin and I. Hanski, eds. *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, London.
- Hastings, A., and T. Powell. 1991. Chaos in a three-species food chain. *Ecology* 72:896–903.
- Neubert, M. G., and M. Kot. 1992. The subcritical collapse of predator populations in discrete-time predator-prey models. *Mathematical Biosciences* 110:45–66.
- Rössler, O. 1976. Different types of chaos in two simple differential equations. *Zeitschrift für Naturforschung Teil A* 31:1664–1670.
- Soulé, M. E. 1987. *Viable populations for conservation*. Cambridge University Press, Cambridge.
- Thompson, J. M. T., and H. B. Stewart. 1986. *Nonlinear dynamics and chaos*. Wiley, New York.
- Ueda, Y. 1980. Explosion of strange attractors exhibited by Duffing's equation. *Annals of the New York Academy of Sciences* 375:422–434.
- Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. *American Naturalist* 139:1151–1175.

KEVIN MCCANN
PETER YODZIS

DEPARTMENT OF ZOOLOGY
UNIVERSITY OF GUELPH
GUELPH, ONTARIO N1G 2W1
CANADA

Submitted April 12, 1993; Revised February 9, 1994; Accepted February 17, 1994

Associate Editor: John Pastor