Diffusion-induced chaos in a spatial predator–prey system

MERCEDES PASCUAL
Woods Hole Oceanographic Institution, Biology Department, Woods Hole, Massachusetts 02543, U.S.A.

SUMMARY
A continuous predator-prey model in which both species diffuse along a spatial gradient is shown to exhibit temporal chaos at a fixed point in space. The model incorporates a nonlinear functional response of the predator and a logistic growth of the prey; the intrinsic growth rate of the prey varies linearly with space. Numerical results demonstrate that low diffusion values drive an otherwise periodic system into aperiodic behavior with sensitivity to initial conditions. Evidence is provided for a quasiperiodic route to chaos as the diffusion rate decreases. These results suggest that complex temporal dynamics in natural communities may arise through the spatial dimension. Spatially induced chaos may have an important role in spatial pattern generation in heterogeneous environments.

1. INTRODUCTION
A variety of ecological models exhibit chaotic dynamics because of nonlinearities in population growth and interspecific interactions (see, for example, Gilpin 1979; Hastings & Powell 1991; Kot et al. 1992; Schaffer 1988). These models have for the most part ignored space. Explicit consideration of space, however, can fundamentally alter the dynamics of nonlinear interactions (Turing 1952; Levin & Segel 1976).

The few ecological studies of chaos in spatial systems consider models in discrete time and space (Solé & Valls 1992; Hassell et al. 1991) or in discrete time and continuous space (Kot 1989). In all these models, the diffusive dispersal of organisms drives a predator–prey or a host–parasitoid system into chaotic dynamics.

The results of discrete models cannot be applied directly to nonlinear interactions and dispersal in continuous time and space. It is well known that discrete models exhibit chaos more readily than their continuous counterparts. For instance, chaotic dynamics is possible for discrete time models of even a single species, but require at least three variables in continuous time.

In this paper I investigate the behavior of a continuous predator–prey system on a spatial gradient that affects the intrinsic growth rate of the prey. This model differs from most reaction–diffusion models because space is heterogeneous rather than homogeneous. It differs from coupled map lattices and other discrete models because it is continuous in both time and space. Unlike the discrete-time models underlying coupled map lattices, the predator–prey models used here cannot exhibit chaos in the absence of spatial diffusion. Thus any chaotic behavior must result from the interaction of the (non-chaotic) local dynamics with the spatial gradient.

Simulations of the model have shown that diffusion can drive predator and prey numbers into complex patterns of variability in time. The main goal of my work is to determine if these patterns are chaotic. I demonstrate with a variety of approaches, including bifurcation diagrams, correlation dimension estimates and Poincaré sections of reconstructed attractors, temporal power spectra, and dominant Lyapunov exponents, that predator and prey numbers at a fixed spatial location exhibit temporal chaos and quasi-periodicity. At some spatial scales these results may apply to planktonic organisms transported by turbulent diffusion.

2. THE MODEL
To pose the problem in its simplest form, consider a single spatial dimension along which both species diffuse at the same constant rate $D$. At any point $X$ and time $T$, the dynamics of the prey ($P(X,T)$) and predator ($H(X,T)$) populations are given by a reaction–diffusion model with logistic growth of the prey and a type II functional response of the predator:

$$
\frac{\partial P}{\partial T} = R_x P \left( \frac{1 - P}{K} \right) - \frac{AC_1 P}{C_4 + P} H + D \frac{\partial^2 P}{\partial X^2}
$$

$$
\frac{\partial H}{\partial T} = \frac{C_1 P}{C_4 + P} H - MH + D \frac{\partial^2 H}{\partial X^2}.
$$

The parameters $R_x$, $K$, $M$ and $1/A$ denote the intrinsic growth rate and carrying capacity of the prey, the death rate of the predator, and the yield coefficient of prey to predator, respectively. The constants $C_1$ and $C_4$ parameterize the saturating functional response.

To describe an environment surrounded by dispersal barriers, I assume zero flux at the boundaries. Hence, at $X = 0$ and $X = L$,

$$
\frac{\partial P}{\partial X} = \frac{\partial H}{\partial X} = 0 \text{ for all } T.
$$

In the absence of diffusion, system (1) is a standard predator–prey system, which exhibits stable equilibria or limit cycles (May 1973).
A simple form of environmental heterogeneity can be introduced by allowing the parameters in (1) to vary with $X$. In this paper I consider the case where the prey rate of increase $R_x$ is a linear function of $X$.

This paper is concerned with the effects of diffusion and heterogeneity on a system which, in the absence of those factors, exhibits limit cycle dynamics. There is considerable literature on the related problem of the diffusive instability of fixed points (Turing 1952; Murray 1989; see Levin & Segel (1976) for a predator–prey example). It is worth noting here that the conditions for such instabilities are not satisfied by system (1) (see Discussion).

The model can be simplified by introducing the dimensionless variables $p = P/K$ and $h = AH/K$. Space is scaled by the total length of the gradient $L$, and time is scaled by a characteristic value of the prey growth rate $R$. Thus, $x = X/L$ and $t = RT$ where $R = R_x(X_0)$ for some $X_0$ in $[0, L)$. System (1) becomes

$$
\begin{align*}
\frac{\partial p}{\partial t} &= r_p(1-p) - \frac{ap}{1+bp}h + d \frac{\partial^2 p}{\partial x^2} \\
\frac{\partial h}{\partial t} &= -mh + d \frac{\partial^2 h}{\partial x^2}
\end{align*}
$$

where the new parameters are

$$
\begin{align*}
&\gamma = \frac{R_x}{\bar{R}} = \gamma + f, & a = \frac{C_2 r K}{C_1 R}, & b = \frac{K}{C_2}, \\
&m = M/R, & d = D/L^2 R.
\end{align*}
$$

At the boundaries, now given by $x = 0$ and $x = 1$,

$$
\frac{\partial p}{\partial x} = \frac{\partial h}{\partial x} = 0 \quad \text{for all } t.
$$

3. NUMERICAL METHODS

Although the dynamics of system (1) in the absence of diffusion are well understood, there is little analytic theory for the system in space. The equations were integrated numerically with an implicit scheme using 100 spatial grid sites. This scheme combines a fully implicit method for the diffusion terms (Roache 1972), with a fourth-order Runge-Kutta method for the predator–prey interaction terms.

For nonlinear equations, the discretization introduced by numerical methods may generate spurious results. To test this possibility, the resolution of the simulations was increased in space and time, and the system was integrated with a different numerical scheme, a finite difference method (forward in time and centred in space). In all cases the same qualitative results were obtained.

In the absence of diffusion, the simulations match the known behaviour of the system, i.e. stable equilibria or limit cycles. The accuracy of these periodic solutions was used as a criterion for periodicity. If successive maxima coincided to the fourth decimal place, solutions were considered periodic.

4. RESULTS

The results presented here are based on numerical analysis for a set of parameters ($a = 5$, $b = 5$, $m = 0.6$, $\varepsilon = 2$ and $f = -1.4$), chosen to obtain limit cycles at each fixed location along the gradient in the absence of diffusion. One diffusion rate ($d = 10^{-4}$), was initially studied. Figure 1 illustrates the irregular temporal and spatial behaviour of prey numbers after transients have died out. Predator and prey densities at any fixed location in space are aperiodic in time (figure 2) and show sensitivity to initial conditions (figure 3). The following results focus on characterizing these irregular motions, determining if they are quasiperiodic or chaotic, and documenting the bifurcations produced by changes in the diffusion rate.

Transitions to chaotic behaviour are known to occur.

![Figure 1](image1)

**Figure 1.** Complex spatiotemporal patterns in prey density after transients have died out ($d = 10^{-4}$).

![Figure 2](image2)

**Figure 2.** Irregular temporal behaviour of (a) prey and (b) predator densities at location $x = 0.85$ ($d = 10^{-4}$).

![Figure 3](image3)

**Figure 3.** Sensitivity to initial conditions. Temporal solutions diverge for small initial differences. Trajectories of prey numbers at $x = 0.85$ are shown for two initial conditions differing by 0.001 in both $p$ and $h$ at every $x$ ($d = 10^{-4}$).
along different routes as a parameter is varied (Schaffer 1988; Schuster 1984). Identifying one of these known routes provides a diagnostic for chaos. The diffusion rate \( d \) was varied in a range that covered a rich range of dynamics including not only the irregular behaviour described above but also periodic solutions. System (2) exhibits periodicity at both low and large values of \( d \) (\( d \approx 10^{-4} \) and \( d \approx 3 \times 10^{-3} \), respectively). To obtain a bifurcation diagram, successive local maxima at a fixed location were plotted as a function of the corresponding diffusion rate for \( 10^{-4} < d < 3 \times 10^{-3} \) (figure 4). A period 1 trajectory produces a single point. More generally, periodic trajectories produce finite numbers of points. Successive maxima of quasiperiodic and chaotic trajectories spread over a range of values. Whereas the former densely cover this range, the latter present a complex structure. Note the different qualitative regions in the diagram. For large values of the diffusion rate, dynamics are periodic (figure 4a). For smaller values of \( d \), periodicity is lost and the maxima visit a whole segment (figure 4a, b). At two points in the diagram, the maxima suddenly scatter on a larger segment (see arrows in figure 4c, d). Where windows appear, trajectories become periodic again (see figure 4c, for \( d \approx 5 \times 10^{-4} \)). The windows in the diagram were investigated at a higher resolution in \( d \). Results (not shown here) reveal clearly periodic behaviour within these windows over a range of \( d \) values. Figure 4 is thus reminiscent of the quasiperiodic route to chaos. In this route, a bifurcation occurs by adding a second frequency to a periodic motion. The attractor of the system becomes a two-dimensional manifold, the surface of a torus. When the ratio of these two frequencies is rational the trajectory on this surface closes after a finite number of cycles. This periodic motion is called a frequency-locked state. For an irrational ratio the motion is called quasiperiodic; the trajectory never closes and covers the whole torus. After quasiperiodicity, a transition to chaos and the break up of the torus into a strange attractor becomes possible (Schuster 1984).

Visualising the system’s attractor would allow this hypothetical scenario to be investigated. The infinite dimensionality of system (2) precludes a simple plot of trajectories in phase space. However, if the attractor itself is low dimensional, it may be reconstructed from knowledge of a single variable (Takens 1981; for ecological discussion see Kot et al. (1988)). Suppose that the attractor lies in an \( n \)-dimensional space, but that one follows only the dynamics of a single variable \( z(t) \). Then, for almost every time lag \( \tau \), the attractor of the \( E \)-dimensional time series

\[
Z(t) = [z(t), z(t+\tau), z(t+2\tau), \ldots, z(t+(E-1)\tau)]
\]

is qualitatively the same as the unknown attractor of the \( n \)-dimensional system (Takens 1981; Kot et al. [1993]).
Figure 5. Log–log plots of the correlation sum $C(r)$ as a function of length scale $r$ for various embedding dimensions.
(a) $d = 10^{-3}$ and $E = 2, 3, \ldots, 6$. (b) $d = 10^{-4}$ and $E = 3, 4, \ldots, 10$.

Figure 6. Reconstruction of the attractor in three dimensions from trajectory of prey numbers at $x = 0.85$.
(a) Aperiodic motion on a torus ($d = 10^{-3}$). (b) Periodic motion on a torus ($d = 5.06 \times 10^{-4}$). (c) Aperiodic motion on the projection of a strange attractor ($d = 10^{-4}$).

The ‘embedding dimension’ $E$, which needs to be sufficiently high but not larger than $2n+1$, corresponds to the notion of degrees of freedom, in the sense of providing a sufficient number of variables to specify a point on the attractor (Farmer 1982).

Theoretical and numerical results have shown that the attractors of many infinite-dimensional dynamical systems are of finite dimension (Farmer 1982). To explore this possibility for system (2), the fractal dimension of the attractor was estimated by computing its correlation dimension $D_c$ (Grassberger & Procaccia 1983). (A description of the algorithm can be found in Bingham & Kot (1989).) Figure 5 shows log–log plots of the correlation sum against length scale. These curves exhibit linear regions with slopes that provide an estimate of the correlation dimension $D_c$. This quantity was computed for increasing values of $E$ until convergence occurred. For $d = 10^{-3}$, the estimated correlation dimension converged to a value of 2.0 (characteristic of motion on a torus) for $E \geq 3$. Thus three dimensions appear to be the minimum number needed to reconstruct the attractor. For $d = 10^{-4}$, which produced the complex dynamics of figures 1–3, the attractor’s dimension converged to $D_c = 3.2$ for $E \geq 7$. The fractional dimension is characteristic of strange attractors. For $d = 10^{-5}$, then, $E = 3$ is certainly too low, but may still provide information on qualitative changes in dynamics.

The attractor was reconstructed in three dimensions from the time series of prey densities at the fixed location $x = 0.85$ for decreasing values of $d$. After the loss of periodicity, the reconstructed trajectories appear to move on a torus (figure 6a). In the windows of the bifurcation diagram, frequency locking occurs (figure 6b). As $d$ decreases, the reconstruction, now only a projection of the attractor, becomes more complex (figure 6c).

Cutting the reconstructed trajectory with a plane and following those points in the orbit that intersect the plane yields a Poincaré section which transforms a continuous flow into a discrete map of lower dimension (Kot et al. 1988). The Poincaré section of a torus is a one-dimensional curve topologically equivalent to a circle. When frequency locking occurs, the Poincaré section reduces to a finite set of points. Figure 7a, b shows these phenomena for the attractors of figure 6a, b. As $d$ decreases, the torus breaks up into a more complex attractor (figure 7c). This occurs at the values of $d$ where the maxima scatter into larger regions in the bifurcation diagram. Given the low embedding dimension, this qualitative change could correspond to chaos or motion on a higher dimensional torus. The former is supported by the non-integer value of the correlation dimension.

Further evidence for chaos is provided by the power spectra of the system. The power spectra of the quasiperiodic behaviour at a fixed location exhibits sharp peaks corresponding to the fundamental frequencies and their harmonics (figure 8a). Notice the increase in background noise levels when $d$ decreases (figure 8b). Such continuous, broadband spectra are characteristic of chaos.

Suggestive as these results may be, many authors consider sensitivity to initial conditions to be the crucial defining feature of chaos. The sensitivity apparent in figure 3 was quantified by calculating the
of behaviour for this predator–prey interaction. Previous ecological examples of chaos in spatial systems consider discrete maps for one or two species, a class of models already capable of complex dynamics with no spatial dimension (Kot 1989; Solé & Valls 1992).

The spatial distributions of predator and prey in this model are not simple reflections of the underlying environmental gradient. Because of nonlinearities, environmental variability is transferred to other spatial scales (see figure 1). The resulting pattern reflects the non-separable effects of the environment and the biology. An attempt to classify the pattern as autonomous against induced, or physical against biological, would clearly fail.

These results differ in several ways from previous studies of pattern formation with reaction–diffusion equations in ecology (Murray 1989). Those studies have shown that coupling diffusion to nonlinear ecological interactions can generate spatial pattern (Okubo 1980). When inhibiting factors (e.g. predators) disperse faster than do activating factors (e.g. prey), diffusion can drive the system into a new asymptotic state that is non-uniform in space (Levin & Segel 1976; Segel & Jackson 1972). In all ecological examples of such diffusive instabilities, the resulting spatial pattern has been either constant or periodic in time (Levin & Segel 1985; Kishimoto et al. 1983). By contrast, system (1) produces chaotic dynamics and spatial patterns that are continuously changing and exhibit long-term unpredictability.

In addition, two-species predator–prey systems exhibit diffusive instabilities only under special conditions (autocatalytic prey growth rates (Levin & Segel 1976), Allee effects (Mimura & Murray 1978), or density-dependent predator death rate (Okubo 1980)). None of these conditions are needed for the generation of spatial pattern in this model. System (1) describes the predator–prey interaction with a standard set of terms commonly used in ecology (May 1973).

Many studies of predator–prey or host–parasitoid systems in heterogeneous environments have concluded that dispersal is a stabilizing influence, one that moderates temporal fluctuations (Hastings 1982; McMurtrie 1978; Taylor 1990). The spatial coupling of local fluctuations may give rise to stable equilibria or reduce the amplitude of the oscillations at the local and regional levels (Comins & Blatt 1974; Crowley 1981; McLaughlin & Roughgarden 1991). In this study, in contrast, local oscillations give rise to complex temporal dynamics.

The scaled diffusion coefficient $d$ is a critical parameter for this qualitative change in dynamics. Chaos and quasiperiodicity occur for $d$ on the order of $10^{-2}$ to $10^{-4}$. These orders of magnitude are plausible for turbulent diffusion in aquatic environments. For example, with a characteristic growth rate $R = 10^{-2} \text{s}^{-1}$ (or one division per day, typical of phytoplankton growth), the diffusion rate $D$ must satisfy $D/J^2 \approx 10^{-4}$ or $10^{-6}$, to produce a scaled diffusion rate $d$ on the order of $10^{-2}$ to $10^{-4}$. In the horizontal dimension, such values of $D$ occur at spatial scales of $10$–$100$ km (see figure 2A in Okubo (1980)). In the vertical dimension, they become possible at scales of $10$–$50$ m for the lowest
This work was initiated at the 1991 Patch Dynamics Summer School at Cornell University (NSF/OCE 9024396). I am grateful to Thomas Powell for encouragement and advice, Hal Caswell for comments on the manuscript, Cabell Davis for help with the numerical integration scheme, and Mark Kot for suggesting the attractor’s reconstruction and providing programs for the Poincaré sections and dimension estimation. This work was supported by the Education Office of the MIT/WHOI Joint Graduate Program in Oceanography (Ocean Ventures Fund), by NSF Grant OCE-8900231 and ONR Grant No 0014-92-J-1527 to H. Caswell. WHOI contribution number 8219.

REFERENCES


Mimura, M. & Murray, J. D. 1978 On a diffusive


Received 28 September 1992; accepted 12 October 1992